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A STUDY OF THE SHARKS OF THE SUBORDER SQUALOIDEA

By Henry B. Bigelow and William C. Schroeder

With Four Plates

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[1] Contribution 848, Woods Hole Oceanographic Institution.

FOREWORD

The sharks that lack an anal fin but do have snouts of the ordinary "shark" form, and pectoral fins that are wholly posterior to the gill openings (grouped together here as the suborder Squaloidea), have been surveyed of late for Philippine waters and adjacent seas by Fowler (1941) and for the western North Atlantic by Bigelow and Schroeder (1948). But the most recent comprehensive accounts of the group for the oceans as a whole, by Regan (1908) and by Garman (1913, pp. 188-244), now lie many years in the past. And so much additional information has come to hand during these years, from various sources, that the time seems ripe for a fresh survey of the group. Many taxonomic questions, however, still await for their solution the critical examination of large series of specimens. We attempt little more in the following pages than to summarize the present state of knowledge of the group. Anything as ambitious as would be implied by the word "revision" is a task for the future.

It will save repetition if we state here (once and for all) that the names of the species we have seen are preceded by an asterisk (*).

Also, we should remind the reader, who may not be familiar with the use of the trawl in deep water, that the depths of capture reported by this method, under the several genera, are in reality those at which the trawl was dragging on the bottom. This is not necessarily the depth at which the shark in question was living, for it is always possible that any particular specimen (even of the species that hold closest to the bottom) may have been picked up when the trawl was being lowered, or hauled up again through the water. The only precise data in this regard are for specimens caught on hook and line. And we have very few definite records of depths of capture for line-caught sharks.

ACKNOWLEDGMENTS

We welcome the opportunity of thanking our colleagues in different parts of the world who have assisted us in various ways: especially Dr. Tokiharu Abe, Tokyo, for contributing a specimen of *Somniosus longus;* the Australian Museum, through Dr. G. P. Whitley, for a specimen of *Oxynotus bruniensis;* Dr. G. Belloc of the Museum, Monaco, for the gift of an excellent specimen

of *Oxynotus* from Italy; Dr. James Böhlke, of the Academy of Natural Sciences for making available to us for study the type specimen of *Heteroscymnoides marleyi,* from the Natal Coast, southern Africa; the British Museum for the loan of the specimens of *Centroscymnus crepidater* and of *Scymnodon ringens,* on which Günther (1870) based his descriptions of these species, and of a specimen of *Oxynotus paradoxus;* Dr. Paul Budker, of the Paris Museum, for denticles from the type specimen of *Scymnodon obscurus,* and for drawings of its teeth; Dr. Fernando Frade for re-examining for us the type specimen of *Oxynotus paradoxus;* Dr. Arni Fridriksson for specimens of *Centrophorus squamosus* and of *Somniosus microcephalus* from Iceland; Dr. J. A. F. Garrick for kindly allowing us to quote from his manuscripts in advance of publication, for a specimen of a New Zealand shark apparently not separable from *Centroscymnus crepidater* of the eastern North Atlantic and for a paratype of *Etmopterus abernathyi*; Dr. Finnur Gudmundsson, of the Museum of Natural History, Reykjavik, for the loan of an excellent series of *Centroscymnus crepidater* (see p. 91); Col. John K. Howard for specimens of *Squalus megalops* from New South Wales; Mr. N. B. Marshall for notes on *Euprotomicrus* (p. 127); Dr. George S. Myers, of the Natural History Museum, Stanford University, for loaning us a paratype of *Centroscyllium ruscosum;* Mr. G. Palmer, of the British Museum, for contributing tracings of pectoral fins of Richardson's young specimen of *Acanthias vulgaris,* renamed *Squalus megalops* by Regan; Dr. J. R. Pfaff, University Zoological Museum, Copenhagen, for the loan of specimens of *Centrophorus squamosus, Deania calcea,* and *Centroscymnus crepidater,* from Icelandic waters, and for the gift of a specimen of *C. crepidater;* Dr. A. M. Ramalho for many kindnesses, including the contribution of a series of *Oxynotus centrina* from off Portugal and of an excellent specimen of *Echinorhinus brucus* from northwest Africa, also for photographs of a specimen (now in the Bocage Museum in Lisbon) that had been described and pictured in 1870 by Capello under the name *Lacmargus rostratus* Risso 1826; Dr. Leonard Schultz, for making available to us the extensive collections of the U. S. National Museum, as well as for assistance in various other ways; Dr. J. L. B. Smith, Rhodes University, Grahamstown, for photographs of the second dorsal fin spine of the shark described by Gilchrist

1922 as *Atractophorus armatus;* Dr. Ethelwyn Trewavas of the British Museum for contributing a drawing of a lower tooth of the type specimen of *Centroscymnus macracanthus* as well as for constant cooperation; Mr. Denys W. Tucker of the British Museum for drawings of the first and second dorsal fins of the type specimen of *Centroscymnus macracanthus;* and Dr. Gilbert P. Whitley, of the Australian Museum, for making available to us a lower tooth from the type specimen of *Centrophorus harrisonii* and for contributing a tracing of the pectoral fins of the type specimen of *Squalus megalops.*

Drawings are by Eugene N. Fischer, Jessie H. Sawyer and Henry B. Bigelow, except as otherwise noted. Photographs were contributed by the Woods Hole Oceanographic Institution.

CLASSIFICATION OF THE SQUALOIDEA

While the sharks in question are an extremely homogeneous assemblage differing conspicuously in their general makeup from the other groups of sharks with which they share the lack of an anal fin (pristiophoroids and squatinoids), the taxonomic ranking assigned to them by recent authors has reflected divergent viewpoints. Thus they have been grouped with the pristiophoroids by Garman (1913, pp. 12, 13) as the "group of families" Squaloidei; by Berg (1940; Eng. Trans. 1947, p. 381) as the suborder Squaloidei; by White (1937, pp. 100, 101) as the suborder Squalida; and by Bertin (1939, pp. 17-19) as the suborder Squaliformes. Fowler (1941, pp. 222, 279) has placed the squaloids in a separate order (Cyclospondyli), joining the pristiophoroids with the squatinoids as the order Squatinae. Bigelow and Schroeder (1948, p. 77) classed the squaloids as one suborder (Squaloidea), the pristiophoroids as a second suborder (Pristiophoroidea), and the squatinoids as a third suborder (Squatinoidea) of the order Selachii. Still more recently Berg, 1955, while similarly classifying the squaloids and the squatinoids as suborders, has set the pristiophoroids apart as a separate order. And this arrangement has much to recommend it for the pristiophoroids are distinguished not only by their sawlike snout, but by the "presence of a separate antorbital bar, from which the upper jaw is suspended by a broad ligament, in addition to the articulation to the cranium" (Bigelow and Schroeder, 1948, p. 532).

Characters. Sharks without an anal fin, but with the snout of the ordinary shape (i.e. not beak-like and without lateral teeth or cirri), and subcylindrical in general form, the anterior margins of the pectoral fins not expanded forward past the first pair of gill openings. Two dorsal fins, with or without fin-spines. Only 5 gill openings, all of them anterior to the pectorals. Inner margins of pelvics entirely separate posterior to cloaca. Nostrils entirely separate from mouth. Spiracles present and conspicuous. Eyes without nictitating fold or membrane. (For internal characters, see Bigelow and Schroeder, 1948, p. 449.)

Families. Views have differed as to whether a subdivision of the Squaloidea into separate families is justified on any basis that has yet been proposed. Garman (1913, p. 13) distributed them among three families: Squalidae for those with spines in the dorsal fins, Scymnorhinidae and Echinorhinidae for those without spines, separating these last two, one from the other, by differences in their teeth. And this same scheme was accepted by Bigelow and Schroeder (1948, p. 450), except that they replaced the name Scymnorhinidae by Dalatiidae because the generic name *Scymnorhinus* Bonaparte 1846 is synonymous with *Dalatias* Rafinesque 1810. Bertin (1939), however, recognized only two families among the sharks in question — Squalidae for those with fin spines, and Scymnorhinidae for those without spines — while Berg (1940) has united them all in the single family Squalidae. And Hubbs and McHugh (1951, pp. 163, 164), for the reasons stated on p. 9, follow Berg in their suggestion "that the Dalatiidae be fused with Squalidae" and that the Echinorhinidae "should likewise be synonymized with Squalidae," though they retain the Dalatiinae and Echinorhininae as subfamilies, pending future study.

These differences do not stem from any recent increase in factual knowledge, for the external features of the squaloid sharks were about as well known structurally a hundred years ago as they are today. What the different systems do chiefly mirror is the opinions held by the several authors as to the degrees of consanguinity among the animals in question. The expression, however, of views in this regard is but the secondary purpose of animal classification; the primary purpose, as so trenchantly worded by Simpson (1945, p. 13), is to "provide a convenient practical means by which zoologists may know what

they are talking about and others may find out." In the case of any suborder as homogeneous structurally as the squaloid sharks are, and for which the fossil record throws little light on their evolutionary history, the decision, whether any subdivision into different families is warranted depends primarily (in our opinion) on whether it will help anyone from the practical standpoint. The scheme adopted here is based on this premise. At the same time it also emphasizes the strong probability that one of the genera with which we are here concerned (*Oxynotus*) represents a separate line of descent, for it is set apart from all the others not only by the arrangement of its upper teeth, by the nature of its dermal denticles, and by its body form (p. 14), but also because it was differentiated at least as early as the Miocene.

Oxynotus was made the basis of a separate family (Oxynotidae) by Jordan (1923, p. 103), followed by Rey (1928, p. 467).[2] And this course is followed here, as better indicative of the apparent degrees of genetic relationship among squaloid genera than was our former inclusion of it in the family Squalidae (Bigelow and Schroeder, 1948, p. 450).

The Linnean genus *Squalus*, which includes the common spiny dogfishes, has been regarded as what may be termed the "key genus" among the squaloids that remain after the subtraction of *Oxynotus*. This implies that the ancestors of the modern squaloids had spines in their dorsal fins. And this view, recently urged by Hubbs and McHugh (1951), is at least consistent with the fossil record, for *Protospinax* Woodward 1919, from the Upper Jurassic of Bavaria, with a spine of the squaloid type in each of its dorsal fins, but with a small anal fin (if Woodward's interpretation of the specimen be correct), and with teeth but little differentiated in nature, may in some measure bridge the gap between the squaloid sharks and the galeoids. Hubbs and McHugh further argue that the absence of a spine in the second dorsal fin in such of the sharks in question as lack one (also of a spine in the first dorsal fin in all but one of the genera in question) probably does not point to any close relationship among them, but more likely represents the end result of convergent evolution (i.e. loss of fin spines) along separate phyletic lines leading back to as many separate spiny-finned ancestors. As one illustration, they point out that "com-

[2] Regarded as a subfamily by Fowler, 1941, p. 223.

plete obsolescence of the spines would render *Centroscymnus* scarcely separable from *Somniosus.*" This leads them to conclude that the presence or absence of spines in the dorsal fins has been given undue weight in current classifications of the squaloid sharks (as by Bigelow and Schroeder, 1948) in which it is invoked as the basis for the separation of families. Here the fossil record does not help us at all, for this reaches as far back for the genera *Dalatias* and *Isistius,* which lack fin spines, as for the spiny-finned genera *Squalus, Etmopterus* and *Centrophorus,* i.e. to the Upper Cretaceous — always provided that identification of the fossils in question with these modern genera was correct. For that matter, a shark with a rostral blade (but lacking rostral teeth) that may reasonably be regarded as ancestral to the pristiophoroids (Woodward 1932, p. 476, Pl. 18; see also Jaekel, 1890, for other early pristiophorid fossils) is similarly known from the Upper Cretaceous; *Squatina* is even known from as far back as the Jurassic. Thus both the squaloids with spiny fins and those lacking spines, the progenitors of the pristiophoroids with their bizarre snouts, and the squatinoids (ray-like in appearance though true sharks) had completed their major evolutionary history by the Upper Cretaceous period, which (the geologists tell us) lies something like 75 million years in the past. For all that is known to the contrary, this may equally apply to the aberrant squaloid genera *Oxynotus* and *Echinorhinus,* though the known record for these runs back only to the Miocene. (For the fossil record of modern shark genera, see Romer 1945, pp. 576-577.)

Were one approaching the problem anew, the shape of the caudal fin, combined with the degree of elevation of the caudal axis, would seem about as appropriate as would the presence or absence of fin spines for a primary alternative among the genera of squaloids. Thus the one character is about as susceptible of precise determination as the other, while, in each case, the extreme states are bridged by intermediates so that division is not sharp-cut on either basis. Also the use of either one would result in the same grouping of genera as would the use of the other, with one exception.

A third character that is alternative between the groups of genera under discussion here, though it seems not to have been emphasized previously in this particular connection, is the con-

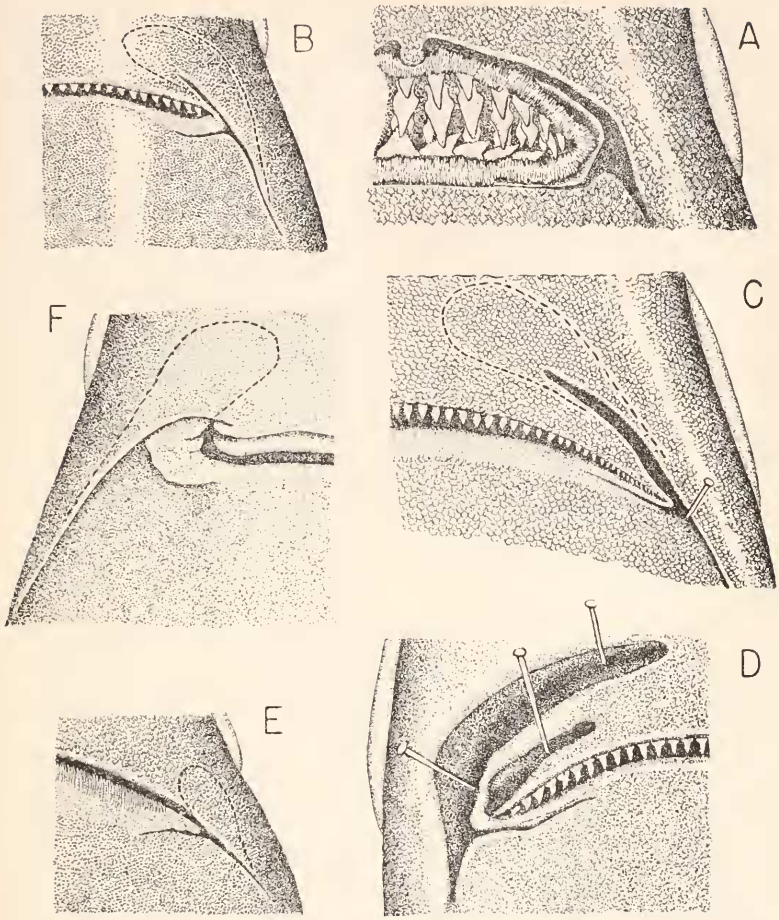

Fig. 1. Corner of mouth, of different squaloids, to show preoral clefts and preoral pouches, if any; the latter outlined by the broken curves. A, *Oxynotus centrina*, male 590 mm. long, Mus. Comp. Zool. No. 39576, x about 3. B, *Centrophorus squamosus*, female 1230 mm. long, Iceland, Mus. Comp. Zool. No. 37825, x about 0.5. C, *Centroscymnus coelolepis*, female, 1035 mm. long, offing of Delaware Bay, Mus. Comp. Zool. No. 38295, x about 2. D, *Centroscymnus crepidater*, female, 784 mm. long, Faroes, Mus. Comp. Zool., No. 39577, with preoral cleft and upper labial furrow pinned open, x about 1. E, *Dalatias licha*, male, 1114 mm. long, Japan, Mus. Comp. Zool. No. 1116, x about 0.5. F, *Isistius brasiliensis*, female, 501 mm. long, Japan, Mus. Comp. Zool. No. 1245, x about 2.

formation of the more or less voluminous inpocketing of the lower surface of the head, that bounds each angle of the jaw on the outer side. In all the known genera of Squaloidea that have a spine in the second dorsal fin as well as in the first (including *Oxynotus,* Fig. 1A), this oral pocket extends inward-forward across the lower surface of the head, anterior to the upper jaw, as an open and conspicuous preoral cleft, that is simple in some (e.g. *Oxynotus,* Fig. 1A; *Centroscymnus crepidater,* Fig. 1D), but that expands inwardly in most to form a more or less voluminous subdermal pouch (e.g. in *Centroscymnus coelolepis,* Fig. 1C). On the other hand, the majority of the genera that lack a spine in the second dorsal fin equally lack the open preoral cleft, although the preoral pouch extending forward from each of the oral pockets is voluminous (Fig. 1E, F). Two, however, of the genera of this group, *Scymnodalatias* and *Echinorhinus* do have short preoral clefts.

And, in any case, the group difference in this respect, while a convenient aid in the definition and identification of genera, is obviously of the kind rated by White (1937, pp. 51-53) as of "physiological importance," rather than as an indication of lines of ancestral descent.

There seems, in short, to be "no securely objective basis," as pointed out by Hubbs and McHugh (1951, p. 163) "on which to choose between the characters to be emphasized" in the classification of the Squaloidea.

But the cause of stability in nomenclature seems best served by using the presence or absence of fin spines as the primary alternative, since this accords with precedent, whereas to use the shape of the caudal fin, as have Hubbs and McHugh (1951, p. 164) in their analytical key to the dalatiine sharks, or to emphasize the presence or absence of the preoral clefts, would result in a novel alignment which we could not support by any cogent reasoning. But we wish it understood that this choice does not carry any phylogenetic implication but is purely a matter of convenience.

In our earlier synopsis of the Squaloidea (Bigelow and Schroeder 1948, p. 450), we recognize two families for such of the genera as lack a fin spine in the second dorsal fin: Dalatiidae for those in which the teeth have only one cusp, but are of conspicuously different shapes in the two jaws, contrasted with

Echinorhinidae (for *Echinorhinus*), in which the teeth are similar in the two jaws, with several cusps. But it seems more logical, in view of the uncertainties just discussed, to follow Hubbs and McHugh (1951) in reducing these categories to the rank of subfamilies of the family Squalidae, the structural contrast between them obviously being much narrower than that between either of them and the genus *Oxynotus* (p. 14).

Key to Families of Squaloidea

Only two or three upper teeth in the first row, but with the number of teeth greater by one in each successive row, so that the rows of functional teeth are successively longer from front to rear; trunk subtriangular in cross section with a prominent ridge low down on either side anterior to the pelvic fins ..... Family Oxynotidae, p. 13

About as many upper teeth in the anterior row as in the succeeding rows, so that any one functional row is about as long as any other; trunk subcylindrical in cross section in most; longitudinal ridges, if any, confined to the tail sector posterior to the pelvic fins .....
Family Squalidae, p. 17

Family OXYNOTIDAE

Family characters (based on only known genus, *Oxynotus*). Squaloidea with the upper teeth occupying a triangular area on the roof of the mouth, in quincuncial arrangement, the functional rows successively longer from front to rear, the first row consisting of three teeth only (on specimen studied, two, according to Rey 1928, p. 469), the number of teeth greater by one in each successive row, and with about six rows functional; lower teeth in a single functional row, blade-like, the median tooth symmetrically triangular, but the successive teeth increasingly oblique, outward (Pl. 1); the uppers smooth-edged, but the lowers finely serrate. The trunk subtriangular in cross section, with a prominent longitudinal ridge low down on either side anterior to the pelvic fins; preoral clefts well developed and very conspicuous, extending forward-inward so far that they are separated by only a narrow isthmus in the midline of the snout (Fig. 1A); lips thick, spongy, with a complex series of cross folds (Fig.

1A); first dorsal fin spine slanting either rearward or forward;[3] the first dorsal fin either with or without supporting radial cartilages posterior to the imbedded portion of the spine; both fin spines conspicuously stout, but projecting only slightly beyond the skin. Dermal denticles so large and prominent that the skin is very rough. On young specimens they are tridentate, with the median point much the longest. But they are much more complex in form on adults, mostly with three subsidiary points, the basal point with a varying number of radial furrows (for excellent illustrations of the denticles, see Rey 1928, p. 471, Fig. 157).

Genera. Only one genus is known: *Oxynotus* Rafinesque 1810.

Remarks. The pattern in which its upper teeth are arranged sets *Oxynotus* apart from all other squaloid sharks — from all other sharks for that matter — which of itself seems to us warrant enough for referring it to a separate family.

Genus OXYNOTUS Rafinesque 1810

Oxynotus Rafinesque, 1810, pp. 45, 60, type species **Squalus centrina* Linnaeus 1758, p. 233, type locality, Mediterranean. For generic synonyms, see Garman, 1913, p. 190.

Generic characters. Those of the family (p. 13). Maximum length probably not far from one meter.

Depth range. The type species (*centrina*) has attracted scientific attention at least since the time of Belon (1515, p. 46 bis), and is well known to Mediterranean fishermen, in moderately deep water. But the only definite statements we have found as to depth of capture are Roule's (1919, p. 123) report of a Mediterranean specimen taken at 60 meters, and Poll's (1951, p. 57) report of three, from 100-180 meters off equatorial West Africa. Depth records for the newly discovered **O. paradoxus* (p. 16) have ranged between 265 and 530 meters (Tucker and Palmer 1949, p. 930). All we have found for **bruniensis* of the Australian-New Zealand region is that a specimen at hand (p. 5) was trawled at about 180 meters.

[3] This seems an appropriate place to remind the reader that it is only the first dorsal fin spine that is inclined forward in any known species of *Oxynotus*, not both of the fin spines, as is erroneously stated in our earlier key to the genera of Squalidae (Bigelow and Schroeder 1948, p. 450, alternative 1A); also that in constructing that key we had overlooked the conditions existing in **O. paradoxus*.

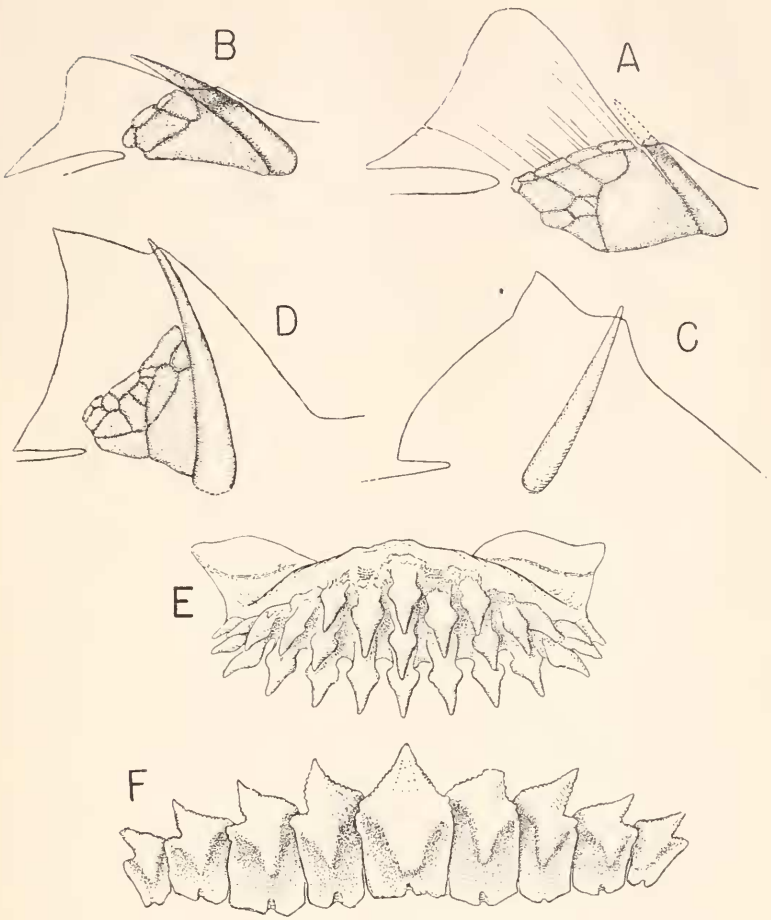

Fig. 2. A, dissection of first dorsal fin of *Squalus acanthias*, female, about 800 mm. long, coast of Massachusetts, Mus. Comp. Zool. No. 458, x about 0.5, to show radial cartilages. B, similar dissection of second dorsal fin of same. C, similar dissection of first dorsal fin of female *Oxynotus centrina*, 640 mm. long, Mediterranean (Mus. Comp. Zool. No. 39564), x about 0.5; D, similar dissection of second dorsal fin of same, x about 0.5; E, *Oxynotus centrina*, male, 590 mm. long, Mus. Comp. Zool. No. 39576, upper jaw and teeth, viewed from in front, x about 3.3; F, lower teeth of same, functional row, viewed from outside the mouth, x about 3.8.

Remarks. Previous to 1929 it had been generally agreed that the forward inclination of the first dorsal fin spine in the two species of *Oxynotus* that had been described up to that time was (with the arrangement of the upper teeth) diagnostic of the genus *Oxynotus,* which still remains the only known representative of the family Oxynotidae. But Frade's discovery in 1929 that the first dorsal spine in his new species **O. paradoxus,* from the coast of Morocco, is inclined rearward (see also Frade 1932 and Norman 1932) has shown that the direction in which it slopes can no longer be regarded as a generic alternative here.

Species. Three species are known: (1) **centrina* (Linnaeus) 1758, familiar to fishermen in the Mediterranean and neighboring parts of the eastern North Atlantic, ranging northward regularly to the Bay of Biscay, also known as a stray to Cornwall (Day 1880-1884, p. 319) and to Norway (Jenkins 1925, p. 321); (2) **bruniensis* (Ogilby) 1893, originally described from Tasmania and subsequently reported from southern Australian waters and from New Zealand; and (3) **paradoxus* Frade 1929, eastern North Atlantic between Morocco and Ireland. For excellent accounts and illustrations of the newly discovered **O. paradoxus,* see Frade 1932 and Norman 1932.

The most conspicuous respects in which these three differ externally one from another are in the shapes of the dorsal fins and in the direction in which the first dorsal spine is slanted. For details we refer the reader to Norman's (1932) illustration and key. A more interesting morphologic difference is that while in **paradoxus* and in **bruniensis* the first dorsal fin posterior to the spine is supported, as in *Squalus* (Fig. 2A, B), by a series of radial cartilages, in **centrina* (Fig. 2C, D) the first dorsal fin has no radial cartilages but is supported solely by the spine.

The dentition also differs in detail from species to species in *Oxynotus,* as is so commonly the case in other genera of sharks. Thus the upper teeth, which are narrow-awl-shaped in the central rows but broadly triangular and blade-like in the outer rows in **centrina* (Pl. 1), are relatively broader in the central rows but relatively narrower in the outer rows in **paradoxus.* Also, the lower teeth differ in number from species to species, there being 9 series in **centrina* (6 specimens counted) contrasted with 13 in the type specimen of **paradoxus,* as Dr. Frade writes us, and 13 (perhaps 15) in the one specimen of the latter that we

have examined (counting is difficult). Rey (1928, Fig. 156, p. 470), it is true, credits **centrina* with 15, and pictures it thus. But this was prior to the discovery of the species **paradoxus*. There are 13 series of lower teeth in the specimen of **bruniensis* we have at hand.

Key to Species of *Oxynotus*

1. First dorsal fin spine sloping a little rearward; distance from tip of second dorsal spine to apex of second dorsal fin is about 1½ times as long as the spine, tip to base ..... **paradoxus* Frade 1929
   Eastern North Atlantic, known off the coasts of Morocco and of Ireland, and from the Gulf of Gascony. For records of occurrence, see Krefft 1955 and Tucker and Palmer 1949.

   First dorsal fin spine sloping forward; distance from tip of second dorsal spine to apex of second dorsal fin is not longer than the spine, tip to base 2
2. Interspace between first and second dorsal fins is at least 1½ times as long as base of second dorsal; distance from tip of first dorsal fin spine to apex of first dorsal fin is only ½-⅔ as long as the spine, tip to base; most, at least, of the dermal denticles on the sides with 3 cusps only ..... **centrina* (Linnaeus) 1758
   Eastern North Atlantic, including the Mediterranean.

   Interspace between first and second dorsal fins little if any longer than base of second fin; distance from tip of first dorsal spine to apex of first dorsal fin is a little longer than the spine, tip to base; most, at least, of the dermal denticles on sides with 5 cusps ..... **bruniensis* (Ogilby) 1893.
   Australia, Tasmania, New Zealand.

Family SQUALIDAE

First dorsal fin, like the second dorsal, with a series of radial supporting cartilages (Fig. 2, A, B); the trunk subcircular in cross section in most (for an exception see under *Cirrhigaleus*, p. 37); upper teeth as well as the lowers in several rows paralleling the jaw, with about as many teeth in any one row as in any other; dermal denticles with one central cusp (if any) in

most, with several cusps in some (p. 18); preoral clefts present in some, but lacking in others; see discussion, p. 12.

Key to Subfamilies of Squalidae

1. Each of the dorsal fins has a spine; preoral clefts present in all known genera, see discussion, p. 12; lips smooth ..... Subfamily Squalinae,[4] p. 18

   No spine in the second dorsal fin or in the first in most cases; preoral clefts lacking in most genera but present in some (see discussion, p. 12) 2

2. Teeth with only one cusp, the lowers much broader than the uppers; lips crenulate or smooth; dermal denticles with only one cusp or spine (if any) ..... Subfamily Dalatiinae, p. 109

   Teeth with several cusps, the uppers similar in shape to the lowers; dermal denticles often with two or more cusps or spines; lips smooth .. Subfamily Echinorhininae, p. 134

Subfamily SQUALINAE

Characters. Squalidae with a spine in each of the dorsal fins; the caudal axis raised, and the caudal fin wider below axis than above; longtitudinal dermal ridges, if any, confined to tail sector, posterior to level of cloaca; preoral clefts present in all known genera.

Remarks. Fowler (1934, p. 239; 1941, p. 223) restricted the subfamily Squalinae to those Squalidae in which the fin spines are not laterally grooved, and in which the caudal fin does not have a subterminal notch, to include *Squalus* Linnaeus 1758, and the barbel-bearing *Cirrhigaleus* Tanaka 1912. For those with laterally grooved fin spines and caudal fin with subterminal notch, he proposed Etmopterinae to include all the other known members of the group. But this scheme results in the union (as Etmopterinae) of species in which the upper teeth have at least three cusps (the lowers also in some) with other species in which the uppers, like the lowers, have only one cusp, a dental difference

[4] Previous to 1896 the sharks in question had commonly been referred to as Spinacidae or as Spinaces; e.g., by Müller and Henle 1841, by Bocage and Capello 1866, by Dumeril 1865, by Day 1880-1884, by Moreau 1881, and by Smitt 1895. The "Centrophoroidei" of Bleeker 1860 was an equivalent. The substitution of Squalidae by Jordan and Evermann 1896 doubtless stemmed from their realization that the generic name *Spinax* Cuvier 1817 was not available as the basis for the name of a family because it is a synonym of *Etmopterus* Rafinesque 1810.

that would seem as sound a basis for subdivision as is the nature of the fin-spines. And the use of the shape of the terminal part of the caudal fin as a primary character here seems forbidden by the differences in this respect among the species which (by their dentition) fall within the genera *Centroscymnus* and *Scymnodon*.

Genera. The members of the subfamily Squalinae as here defined fall in three divisions, as follows:

Division A — Fin spines without lateral grooves; lower contour of caudal fin without subterminal notch; teeth with only one cusp, the cusps of the uppers as well as of the lowers so strongly oblique as to form a nearly unbroken cutting edge along the jaw; the median tooth in each jaw basally overlapping the tooth next to it on either side, and the base of each succeeding tooth overlapping that of the next tooth outward along the jaw. This division includes the genera *Squalus* Linnaeus 1758 and *Cirrhigaleus* Tanaka 1912.

Division B — Fin spines with lateral grooves; lower contour of caudal fin with subterminal notch; upper teeth with three or more cusps, not overlapping basally, the lowers similar to the uppers in some (*Centroscyllium*), but with only one cusp in others (*Etmopterus*), and overlapping basally as in division A. This division includes two well-marked genera: *Centroscyllium* Müller and Henle 1841 and *Etmopterus* Rafinesque 1810.

Division C — Fin spines with lateral grooves and lower contour of caudal with subterminal notch (at least in most cases) as in division B; but teeth (uppers as well as lowers) with only one cusp; the uppers narrower than the lowers in most, either loosely spaced or with their bases in contact or slightly overlapping, the lowers broad based, with each tooth overlapping the next outward along the jaw as in division A. This group includes all known members of the subfamily other than those listed above for divisions A and B.

Students of sharks are now in general agreement as to the alternative characters of the genera *Squalus, Cirrhigaleus* (if the latter be accepted as distinct from *Squalus* — see p. 37), *Etmopterus* and *Centroscyllium;* i. e., divisions A and B. But the picture is not yet clear for the members of division C, which are deep-water species, few specimens of which have found their way into museum collections.

The members of division C that were set apart the earliest from the old genus *Squalus* Linnaeus 1758 were **S. squamosus* Bonnaterre 1788, and **S. granulosus* Bloch and Schneider 1801, both of which were transferred by Blainville (1816, p. 121) to his new genus *Acanthorhinus,* while *squamosus* was referred almost simultaneously by Cuvier (1817, p. 130, footnote 3) to his *Centrina.* But the earliest genus that was based in so many words on a member of this division was *Centrophorus,* proposed by Müller and Henle in 1837, for **C. granulosus* Müller and Henle, which they considered identical with **Squalus granulosus* Bloch and Schneider 1801. And their subsequent description and illustration of it (Müller and Henle 1841, p. 89, Pl. 33) were so satisfactory that there is no doubt as to the specific identity of the Mediterranean specimen which they had at hand.

A year later Bonaparte (1838, p. 207; 1839, p. 9, extra) proposed the generic name *Lepidorhinus* for **squamosus,* while Lowe in 1839 instituted *Acanthidium* for two Madeiran species, one of which (**calceum* Lowe 1839) falls in the group with which we are dealing, whereas the other (*pusillum* Lowe 1839) is now known to be an *Etmopterus* (p. 49).

Next, Gill (1862, pp. 496, 498) made the **Squalus uyato* of Rafinesque 1810 the basis of a new genus, *Entoxychirus,* setting it off from the old genus *Squalus* by its fins, from *Centrophorus* Müller and Henle 1837 under the misconception that the teeth of **uyato* are equally oblique in both jaws. This error was no doubt based on an illustration that Bonaparte (1841, Pl. 57, fig. 2) credited to **uyato,* but which actually pictured the teeth of a *Squalus,* as Garman (1913, p. 198) has pointed out. The relegation of *Entoxychirus* to the synonymy of *Centrophorus* by Garman (1913, p. 196), but its revival by Fowler (1941, p. 242) for species with "pectoral angle extended," contrasted with "not or scarcely extended" in *Centrophorus,* covers the subsequent history of the genus.

In 1864, Bocage and Capello proposed two new genera for members of the division in question: *Centroscymnus,* type species **C. coelolepis* Bocage and Capello 1864, and *Scymnodon,* type species **S. ringens* Bocage and Capello 1864, based in each case on a newly discovered shark from deep water off Portugal. These species were described by them in greater detail, with excellent illustrations two years later (Bocage and Capello 1866, pp. 30,

32, Pl. 1, fig. 1, Pl. 2, fig. 3, Pl. 3, figs, 2a 2b). And while Günther (1870, p. 420) did not regard the dental differences on which these two genera were based as sufficient to separate them from *Centrophorus*, Garman (1906, p. 204) and Regan (1908, p. 39) revived them, Garman without stating his reasons, but Regan because of the same dental characters on which Bocage and Capello had set them up originally.

Meantime, Johnson, in 1867, had proposed the genus *Machephilus* for his new Madeiran species *dumerili*, separating it from *Centrophorus* because of the presence of a symmetrical median tooth in its lower jaw. However, subsequent authors (Garman 1913, p. 212; Rey 1928, p. 440; Bigelow, Schroeder and Springer 1953, p. 224) have classed *dumerili* as a synonym of **Centrophorus squamosus* (Bonnaterre) 1788, i.e., have not considered the presence or absence of a symmetrical median lower tooth as sufficient ground for generic separation, and this same course is followed here (p. 72).

The next landmark in the taxonomic history of the squaline sharks of division C was the institution by Jordan and Snyder in 1902 of the genus *Deania*, type species **eglantina* Jordan and Snyder, a Japanese shark characterized by a very long snout as well as by pitchfork-shaped denticles on the sides of its trunk. And this generic entity was accepted by Garman (1906, p. 205; 1913, p. 215). But Garman's revival of the generic name *Acanthidium* Lowe 1839 for it, in place of *Deania*, was not well judged, for the type species of *Acanthidium* (**pusillum* Lowe 1839) as designated by Goode and Bean (1895, p. 10), by Jordan and Evermann (1896, p. 55), and by Jordan (1919, p. 195) falls within the limits commonly accepted for the genus *Etmopterus* Rafinesque 1810. Consequently, Fowler's (1941, p. 237) relegation of *Acanthidium* to the synonymy of *Etmopterus* is to be accepted — unless indeed Whitley's (1939, p. 266) separation of *Acanthidium*, type species *Centrina nigra* Lowe 1834 (**Acanthiduim pusillum* Lowe 1839[5]) from *Etmopterus* Rafinesque 1810, type species **Squalus spinax* Linnaeus 1758, is to be followed. And the grounds stated by Whitley (i.e. *Acanthidium* with "first dorsal much smaller than the second and the ventrals just before the level of the first dorsal") do not seem to justify

[5] Whitley (1939, p. 266) points out that it was as *Centrina nigra* that Lowe (1834, p. 144) first reported the shark which he renamed **Acanthidium pusillum* in 1839.

generic division in this case, for the relationship in size between the first and second dorsals is about the same among our Norwegian and Mediterranean specimens of **spinax* (type species of *Etmopterus*) as it is in the type species of Lowe's (1839) genus *Acanthidium*. Also, the rear end of the bases of the pelvics ranges in position from below the second dorsal spine to considerably anterior to the latter among the several Atlantic species of *Etmopterus* (Bigelow, Schroeder and Springer 1953, p. 272).

A year after the genus *Deania* had been proposed by Jordan and Snyder (1902), Jordan and Fowler (1903, p. 633) made the Japanese *Centrophorus squamulosus* Günther 1877 the type of still another genus, *Zameus*, separating it from *Centrophorus* by the shape of its dermal denticles. And while Garman (1913, p. 207) classed *Zameus* unequivocally as a synonym of *Scymnodon* Bocage and Capello 1864, Fowler (1941, p. 226) has revived it as a subgenus of the latter, now invoking the length of the orbit as compared with the length of the snout as the alternative subgeneric character.

Next Smith and Radcliffe (1912, p. 681) made their new Philippine species **profundorum* the type of another new genus, *Nasisqualus*, but without mentioning anything to separate it from *Deania* Jordan and Snyder 1902, with which Regan (1912) has synonomized it. And during the following year Garman (1913, p. 206) proposed *Centroselachus* for the Portuguese shark that Bocage and Capello (1864, 1866) had originally described and pictured as **Centrophorus crepidater*, basing its generic separation from *Centrophorus* Bocage and Capello 1864, and from *Scymnodon* Bocage and Capello 1864 on small differenees in the shapes of the dermal denticles. Garman (1913, pp. 189, 211) also revived the genus *Lepidorhinus* Bonaparte 1838, type species **Squalus squamosus* Bonnaterre 1788, but this revival has not been accepted generally.

Nine years after the appearance of Garman's monograph, Gilchrist (1922, p. 48, Pl. 7, fig. 3) proposed the genus *Atractophorus* for a southern African squalid, *A. armatus* Gilchrist, in which the tip of the second dorsal fin spine is described as barbed, like an arrowhead (p. 82). Next Whitley (1932, p. 326) proposed *Deaniops*, with the Australian *Acanthidium quadrispinosum* McCulloch 1915 as type, without including any generic diagnosis at the time, but adding subsequently (Whitley 1939,

p. 266) that it was for "species with a long low first dorsal fin." Two years later Fowler (1934, p. 293) proposed *Proscymnodon*, type species *Centrophorus plunketi* Waite 1909, from New Zealand, as a subgenus of *Scymnodon,* because of length of orbit combined with the positions of the first and second dorsal fins, and *Proscymnodon* has been accepted by Whitley (1934, p. 199; 1940, p. 142) as a full genus. Whitley (1940, pp. 145, 146) subsequently has proposed two subgenera within the old genus *Centrophorus* Müller and Henle 1837, *Gaboa* (type species *Centrophorus harrisonii* McCulloch 1915, Australia) and *Somnispinax* (type species *Centrophorus nilsoni* Thompson 1930, also from Australia), the former because of "the form of its teeth and denticles," the latter because of smooth edged teeth, "differently shaped denticles, differently shaped snout, fins, etc.," but without more precisely specifying what these differences are. As a final complication, Fowler's (1941, p. 223) definition of *Entoxychirus* as with "inner pectoral angles extended" corresponds to Garman's (1913, p. 189) for *Centrophorus,* while Fowler's for *Centrophorus* ("pectoral angles not or scarcely extended") corresponds to Garman's for *Lepidorhinus.*

To sum up, such of the Squalinae as have grooved fin spines, upper teeth as well as the lowers with only one cusp, and caudal fin with a subterminal notch, have been referred to 18 different genera or subgenera at one time or another. But our own study of a broad representation of the group leads us to conclude that the genera *Centrophorus* Müller and Henle 1837, *Centroscymnus* Bocage and Capello 1864, *Scymnodon* Bocage and Capello 1864, and *Deania* Jordan and Snyder 1902, perhaps with the addition of *Atractophorus* Gilchrist 1922, afford appropriate resting places for all of them — provided that a genus, to be of practical value, must be "separated from other similar units by a decided gap" (Mayr, Linsley and Usinger, 1953, p. 48). And we may add that we subscribe heartily to this proviso.

The characters that have proved the most useful, here, for the definition of genera (because they are the most definitely alternative between groups of species) are: the shapes of the teeth, the shape of the inner corner of the pectoral fins, the relative length of the snout, the length of the exposed portion of the second dorsal fin spine, and perhaps also whether the tip of that spine is smooth or is barbed or otherwise expanded, as it is described

for one member of the group (p. 82). The differences in relative size, and in length at base, of the first and second dorsal fins (sometimes invoked as of generic significance) are not sharply alternative enough to be of much help in this regard. And recent discoveries (p. 87) have also proved that the shape of the dermal denticles on the sides of the trunk is not as reliable a generic criterion here as we had formerly believed. For further details in this last regard, see our earlier discussion (Bigelow and Schroeder 1954, p. 47), to which we should add that as early as 1861 Steenstrup had already pointed out that the dermal denticles of sharks do not persist throughout the life of the individual, as the scales of bony fishes do, but are short lived, to be replaced as they are shed by more newly formed denticles.

Synopsis of Genera of Squalinae

1. Upper teeth as well as the lowers with one cusp only 2
   Upper teeth with 3-7 cusps 7
2. Fin spines well developed, without lateral grooves, caudal fin without subterminal notch, its tip not truncate; upper teeth similar in shape to lowers 3
   Fin spines with lateral grooves; lower margin of caudal fin with a definitely outlined subterminal notch and with its tip more or less truncate, at least in most species; upper teeth differing more or less widely in shape from the lowers, except as noted on pages 26 and 38 4
3. Anterior margin of nostril does not bear a barbel; caudal peduncle with a longitudinal ridge along either side, and with a precaudal pit above but none below; upper teeth, like the lowers, with the successive cusps directed outward strongly along either side of the jaw .....
   Squalus Linnaeus 1758, p. 26
   Anterior margin of nostril with a conspicuous barbel reaching beyond the mouth; caudal peduncle without longitudinal ridges and without precaudal pit; other characters, in general, including teeth, as in *Squalus* ..... *Cirrhigaleus* Tanaka 1912, p. 37
4. Inner corner of pectoral fins angular and more or less extended (see discussion, p. 66); fin spines well developed, the second longer than the first; upper teeth narrower than the lowers and more nearly erect in most cases; lowers directed strongly outward; cutting edge of lower teeth smooth in some but more or less irregularly and finely serrate in others (p. 67, Fig. 9); snout in front of mouth not longer than from mouth to level of origin of pectoral fins; dermal denticles on

sides of body low, block-like, scale-like, or conical .....
Centrophorus Müller and Henle 1837, p. 63
Inner corner of pectoral fins not extended; rounded in most, perhaps quadrate in one known species 5

5. Upper teeth midway along either side of the jaw noticeably longer than those toward center of the mouth (Fig. 13C); first and second dorsal fin spines projecting only slightly beyond the skin; dermal denticles on sides of body low, scale-like, with tridentate rear margin; other characters in general as in *Centroscymnus* (alternative 6; see also p. 85) ..... *Scymnodon* Bocage and Capello 1864. p. 96
Upper teeth midway along either side of jaw only slightly longer than those toward center of mouth (Fig. 12C) 6

6. Snout in front of mouth not longer than from mouth to level of origin of pectoral fins; inner corner of pectoral fins broadly rounded; dorsal fin spines either exposed at the tip or entirely enclosed in the skin; lower teeth smooth-edged, the cusps directed strongly outward; upper teeth lancet-shaped, much narrower than lowers, and more nearly erect; dermal denticles on sides of body scale-like, tridentate or evenly rounded, low in adults of known species but rising more steeply from skin on juveniles of at least one (p. 90); subterminal notch of caudal fin well marked in most species, but indistinct in juveniles of one named species, the parentage of which is not yet definitely known (p. 94) ..... *Centroscymnus* Bocage and Capello, 1864. p. 84
Snout in front of mouth longer than from mouth to level of origin of pectoral fins; inner corner of pectoral fins rounded in most, perhaps quadrate in one of known species (p. 102), but not extended at all; both of the dorsal fin spines well exposed; caudal fin with well marked subterminal notch; teeth smooth edged; the uppers narrow, triangular, on broad bases; the lowers strongly oblique in the females of all known species, but less so in the males of some (p. 103); dermal denticles on sides of body pitchfork shaped, rising steeply from the skin; other characters in general as in *Centrophorus* (p. 63) .....
Deania Jordan and Snyder 1902, p. 101

7. Lower teeth with 3-5 cusps and similar to the uppers in shape; dorsal fin spines well developed, with lateral grooves; caudal fin truncate and with subterminal notch in known species (but see discussion, p. 46); caudal peduncle without precaudal pits or lateral longitudinal ridges; dermal denticles on sides of body slender, thorn-like .....
Centroscyllium Müller and Henle 1837, p. 38
Lower teeth with only one cusp, much wider than uppers; dermal denticles on sides of body bristle- or conical thorn-like to truncate; other characters in general as in *Centroscyllium* .....
Etmopterus Rafinesque 1810. p. 47

Genus SQUALUS Linnaeus 1758

Squalus Linnaeus 1758, p. 233, type species **S. acanthias* Linnaeus, designated by Gill, 1861, p. 369.

For generic synonyms, see Bigelow and Schroeder, p. 452.

Generic characters. Squalinae with fin spines well developed, without lateral grooves; caudal fin without subterminal notch but with well marked lower-anterior lobe; caudal peduncle with a longitudinal ridge along either side, and with a pre-caudal pit above but none below; margin of nostril without barbel; preoral clefts present, slightly expanded inwardly; snout in front of mouth considerably shorter than from front of mouth to origin of pectorals; inner corner of pectoral fins either rounded, subangular, or slightly extended; dermal denticles lanceolate, heart-shaped, or tridentate with sharp tip, and of different shapes on different parts of the trunk as well as from species to species; teeth in both jaws with only one cusp, directed so strongly outward as to form a practically unbroken cutting edge along either half of the jaw; the base of each tooth overlapping that of the next tooth, outward. Maximum length a little more than one meter.

Depth range. The depth range recorded for this genus is from the surface down to about 380 meters. Thus **S. acanthias* (p. 30) occurs in numbers anywhere between the surface and the 160-180 meter level. **S. fernandinus* ranges from close to the surface (reported at 16-20 meters by Poll, 1951, p. 62) down to the maximum depth reported above for its genus, while the center of abundance lies considerably deeper for it than for **acanthias*, to judge from Poll's (1951, p. 61) report of 608 specimens trawled at 220 meters off equatorial West Africa. And it seems that neither **cubensis* (reported from 137-384 meters) nor **megalops* rise, normally, as near to the surface as does **acanthias* or **fernandinus*.

Species. All known representatives of the genus *Squalus* from various parts of the world (under whatever names they may have been reported) seem referable to one or other of three divisions as defined by the shape of the pectoral fins; by the position (farther forward or rearward) of the first dorsal fin; by the presence or absence of a small secondary lobelet on the outer edge of the flap-like expansion of the anterior margin of the nostril;

and by the color pattern. In the following discussion each of these divisions is referred to under the name of its earliest described representative.

The differences in the shape of the pectorals, as outlined below, are so obvious that no further discussion of them is called for just here. Similarly, the position of the first dorsal spine, relative to that of the origin of the pectoral fins, has proved definitely alternative for the specimens yet measured, though with the reservation that measurements of a larger number may eventually narrow the gap in this respect. And the shape of the narial flap seems equally diagnostic for the majority of specimens, though we have seen one individual of the *fernandinus* division where one of the nostrils shows the secondary lobelet, but the other does not — a situation analogous to that of the shape of the inner corner of the pectoral fins in *Centrophorus* (p. 67). But our earlier selection (Bigelow and Schroeder 1948, p. 455; Bigelow, Schroeder and Springer 1953, p. 221) of the midpoint of the bases of the pelvics relative to the positions of the dorsals as a species-criterion was a less happy one, for additional information has shown that in this respect the extremes intergrade. And while the presence of white spots is diagnostic for the specimens that show them, the absence of white markings is not diagnostic, for it has long been known that in the type species of the genus (*acanthias*) these spots tend to fade with growth, while some large specimens show no trace of them.

Synopsis of divisions of *Squalus*

Acanthias division. Inner corner of pectoral fins well rounded: the distal margin not deeply concave; point of emergence from skin of 1st dorsal spine is posterior to 5th gill openings by a distance as long as from anterior margin of eye to 5th gill openings or slightly longer; midpoint of base of pelvics about midway between a perpendicular at point of emergence of 2nd dorsal spine and one at free rear tip of 1st dorsal on most specimens, but nearer to tip of 1st dorsal than to 2nd dorsal spine on one large male from Massachusetts (Mus. Comp. Zool. No. 35863) that we have seen. Anterior narial flap simple, without secondary lobelet on its outer edge. Sides of trunk marked with white spots on small and middle sized specimens, more faintly so on larger ones.

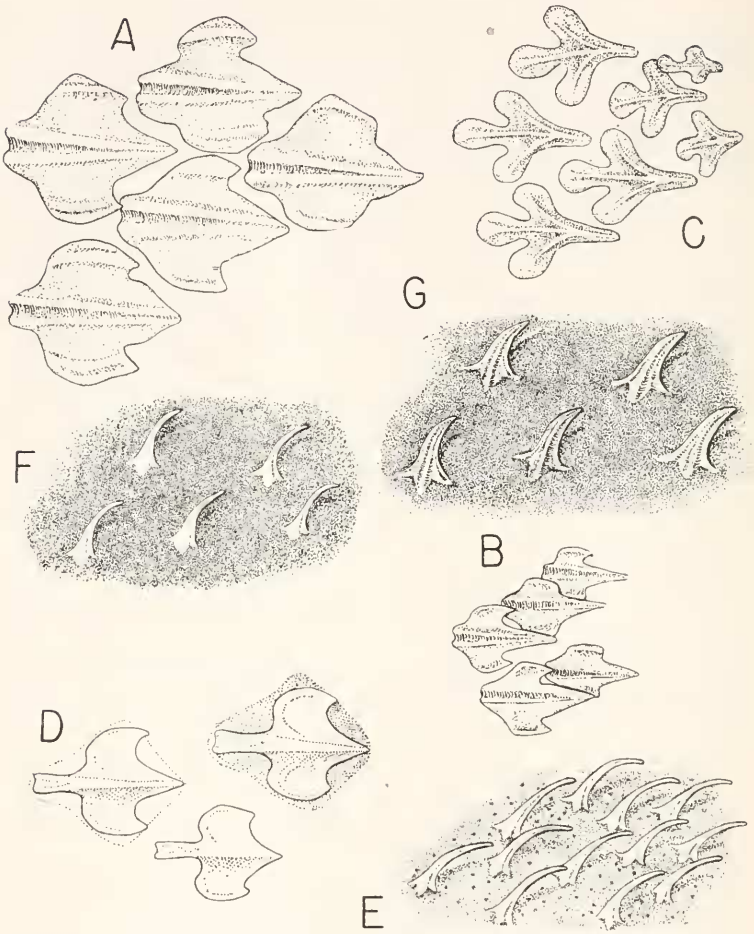

Fig. 3. Dermal denticles from side of body below first dorsal fin. A, *Squalus fernandinus*, female, 914 mm. long, island of Juan Fernandez, Mus. Comp. Zool. No. 841, x about 50. B, *S. fernandinus*, male, 397 mm. long, off South Carolina, Mus. Comp. Zool. No. 37064, x about 50. C, *S. megalops*, same specimen as in Fig. 4A, x about 70. D, *Squalus acanthias*, Massachusetts, x about 34, after Bigelow and Schroeder 1948, Fig. 88C. E, *Etmopterus spinax*, female, 250 mm. long, Norway, Mus. Comp. Zool. No. 1022, x about 15. F, *Etmopterus princeps*, female, 165 mm. long, offing of Nantucket, Mus. Comp. Zool. No. 37403, x about 12. G, *Etmopterus princeps*, female, 610 mm. long, offing of southern edge of Georges Bank, Mus. Comp. Zool. No. 37445, x about 10.

while some adults lack these spots altogether. Dermal denticles on sides below 1st dorsal fin of the shape shown in Figure 3D.

Fernandinus division. Inner corner of pectorals about a right angle, more or less blunted, the distal margin weakly concave; point of emergence from skin of 1st dorsal spine is posterior to 5th gill openings by a distance at least not longer than from anterior edge of eye to 2nd gill openings, and slightly shorter than that in most; midpoint of base of pelvics at least as near to a perpendicular at rear tip of 1st dorsal as to one at emergence from

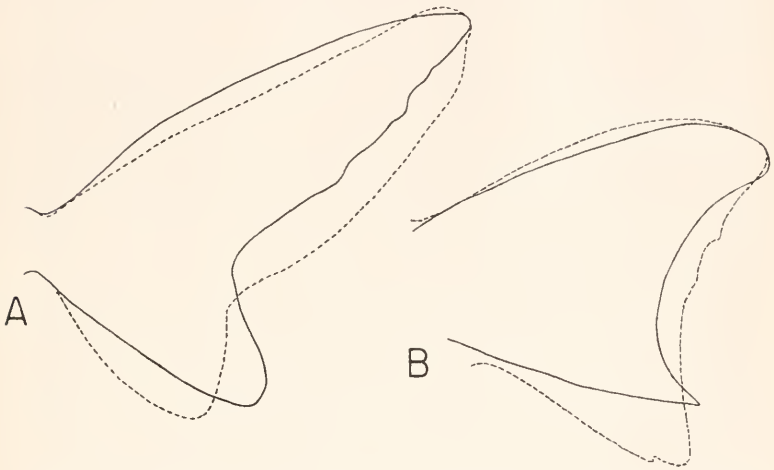

Fig. 4. Outlines of fins of *Squalus megalops* and of *Squalus cubensis*, superimposed to show the differences in shape. A, caudal fins of *S. megalops*, female 526 mm. long, New South Wales, Mus. Comp. Zool. No. 38619 (dotted line), and of *S. cubensis*, female, 672 mm. long, Cuba, Mus. Comp. Zool. No. 1461 (solid line), adjusted to equal lengths along upper margin. B, pectoral fins of *S. megalops* (type specimen), from drawing kindly contributed by Dr. G. P. Whitley (dotted line), and of *S. cubensis*, same specimen as in A (solid line), adjusted to equal lengths along outer margin.

skin of 2nd dorsal spine, and nearer on most (but see above, under *acanthias* division); anterior narial flap with a small secondary lobelet on its outer edge (Bigelow and Schroeder 1948, Fig. 87F), though in occasional specimens this lobelet may be lacking on the one nostril or on the other (see above); dermal denticles on sides below first dorsal fin simpler in form than in

acanthias division, tridentate, the marginal points longer on the denticles of small specimens than on those of larger (Fig. 3, A, B). Trunk without white markings at any stage in growth.

Megalops division. Inner corner of pectoral fin pointed, or only very slightly blunted, the distal margin deeply concave (Fig. 4B); relative positions of fins, shape of narial flap, and color (without spots) essentially as in *fernandinus* division (see above); dermal denticles on sides below first dorsal fin differing from those both of the *acanthias* division and of the *fernandinus* division in a way easier presented pictorially (Fig. 3C) than verbally.

Remarks. There is no danger of confusing any representative of the *megalops* division with any of the *acanthias* division or any of the *fernandinus* division, so sharply diagnostic is the shape of the pectoral fins. But the discontinuity as regards fin characters is so small between the *acanthias* and the *fernandinus* divisions that identification as the one or the other of large plain-colored specimens may call for close scrutiny of the shape of the narial flap and of the denticles.

Acanthias division. **Squalus acanthias* Linnaeus 1758, type species of the genus[6] and locally the most numerous of sharks, represents this division in the North Atlantic, where its regular range extends in the east from Iceland, Norway and the Murman coast to Morocco (including the Mediterranean and the Black Sea), with reports from the Canaries and Senegal; and in the west from southeastern Labrador (straying to southwest Greenland) to the southern part of the North Carolina coast in abundance, with a few ranging to southern Florida and to Cuba.[7]

The common spiny dogfish of the coast of the northwestern Pacific was originally described as a separate species, **suckleyi* Girard 1854, and it has most often been reported under that name. But our own comparison of Californian specimens with others from both sides of the North Atlantic has not revealed any consistent differences that might be regarded as specific, whether in the position of the first dorsal fin relative to the pectorals (the character the most often invoked as alternative), or in any other respect (Bigelow and Schroeder 1948, p. 453).

[6] For synonyms see Bigelow and Schroeder 1948, p. 467.

[7] For details, see Bigelow and Schroeder 1948, pp. 463-464.

Spiny dogfishes of the *acanthias* division have been reported from northeastern Asia both as **acanthias* Linnaeus 1758 and as **suckleyi* Girard 1854; from Japanese waters under the name *vulgaris* Risso 1826, repeatedly as **suckleyi* Girard 1854, as *mitsukurii* Jordan and Fowler 1903 (their illustration, but not their description, which was based on an example of the *fernandinus* division, see below, p. 33), and as *wakiyae* Tanaka 1918, a name proposed by Tanaka for the shark that had been pictured by Jordan and Fowler (1903, p. 630, fig. 3) as *mitsukurii;* from Korea, China and Formosa as *suckleyi.* There is nothing, however, in available information to suggest that these populations differ specifically, one from another, or from the typical **acanthias* of the North Atlantic. Schmidt (1931, p. 7) indeed, has long since expressed a doubt as to whether the spiny dogfishes of the *acanthias* division of Japan are separable from those of the Black Sea. For North Pacific references to *Squalus* of the *acanthias* division, see Bigelow and Schroeder 1948, p. 472.

A representative of the *acanthias* division has also been credited (by name only) to Hawaii (Fowler 1930, p. 495, as *S. suckleyi*). But an earlier report of *mitsukurii* from Hawaiian waters proves actually to have been based on **S. fernandinus* (p. 33).

The *acanthias* division has not been reliably reported for the equatorial-subequatorial belt, whether of the Atlantic or of the Indo-Pacific. But seemingly it is as widespread in mid-latitudes of the southern hemisphere as it is of the northern. Thus sharks apparently of this division have been reported from southern Africa as **acanthias* and as *vulgaris*; from Uruguay and northern Argentina as **acanthias;* from the Magellanic region as **acanthias* and as *lebruni* Vaillant 1888[a]; from Chile as **suckleyi* (by Fowler 1930, p. 495); from New Zealand as **fernandinus* (by Waite 1909, p. 142, Pl. 16, fig. 1) but identity as *acanthias*-like established by rearward position of first dorsal fin and by white spotted sides, and as *kirki* Phillipps 1931; from Australia as *vulgaris* (repeatedly) and as *whitleyi* Phillipps 1931 (see also Whitley 1940, p. 193); and from the island of Reunion in the southern Indian Ocean as *vulgaris.* No one of these southern populations, however, has yet been studied in detail, nor has anything developed within the past few years to contradict our

earlier statement (Bigelow and Schroeder 1948, p. 454) that "the relationship of these southern hemisphere forms to one another and to the northern *acanthias* is uncertain."

Fernandinus division. The earliest named representative of this division is *Squalus fernandinus* Molina 1782, originally described from the island of Juan Fernandez off the coast of Chile. And our recent comparison of a female, 520 mm. long (Mus. Comp. Zool. No. 446) from Nice, France, with a **fernandinus* of 914 mm. from the type locality, as well as with others from the Gulf of Mexico and from the offing of South Carolina, has confirmed the conclusion earlier arrived at by Garman (1913, p. 195), by Poll (1951, p. 59), and by Bigelow, Schroeder and Springer (1953, p. 222), that the shark described from the Mediterranean in 1826 by Risso under the species-name *blainvillii* (Risso 1826, p. 133, Pl. 3, fig. 6) is identical with *fernandinus*. This joint species (most often reported as "*blainvillii*") occurs widespread in the Mediterranean, in the Black Sea, and off the open Atlantic coast from Portugal southward to equatorial waters (reported from 6° 31′ S., see Poll 1951, p. 59). And it is to be expected all along the West African seaboard to the southward, for spiny dogfishes apparently identical with **fernandinus* have been reported in abundance in southern African waters, both as *blainvillii* (by Bleeker, 1860, pp. 50, 58, 80, and by Günther 1870, p. 419): as *acutipinnis* Regan 1908 (by Regan 1908[a], p. 248, and by Barnard 1925, p. 48), and as **fernandinus* (by Gilchrist 1922, p. 48, by von Bonde 1924, p. 5, and by Smith 1949, p. 60). **S. fernandinus* is known in the western side of the Atlantic also, both from the offing of South Carolina and in the Gulf of Mexico in the north (Bigelow, Schroeder and Springer 1953, p. 220), and off the coast of Argentina in the south (for locality records from the western South Atlantic, see Bigelow and Schroeder 1948, p. 480). But the number of specimens so far reported from the western side of the Atlantic, north or south, has not been large enough to suggest that **fernandinus* is as plentiful there, or as generally distributed, as it is in the eastern side, and in the Mediterranean.

The reports that have come to hand for **fernandinus* in the Indo-Pacific are numerous enough, and are distributed widely enough to show that it is as widespread there as it is in the Atlantic, not only in the temperate zones both north and south but

in tropical-subtropical latitudes as well. Thus **fernandinus,* or a form so closely allied to it that no significant differences appear from the published accounts, is widespread in Japanese waters, whence it has been reported as *mitsukurii* Jordan and Fowler 1903 (their description, but not their illustration, which was based on a specimen of the *acanthias* division, see above p. 31[8]); repeatedly also as *japonicus* Tanaka 1917 (for an excellent description and illustration, see Tanaka 1917, p. 467, Pl. 30, figs. 366, 367). It has also been described and pictured from southern China by Fang and Wang (1932, pp. 249, 250, fig. 16), not only under the name *mitsukurii* Jordan and Fowler 1903, but also as *brevirostris* Tanaka 1917, though this last name had actually been based on the Japanese representatives of the *megalops* division, not on one of the *fernandinus* division (see below, p. 36).

The specific identity of the spiny dogfishes that had been reported by Snyder (1904, p. 515), by Jordan and Evermann (1905, p. 45), by Gilbert (1905, p. 580), and by Günther (1910, p. 490), from the Hawaiian Islands under the name *mitsukurii* Jordan and Fowler 1903, had remained uncertain, for the brief descriptions seemed equally applicable to the *fernandinus* division of the genus or to the *megalops* division. But our recent examination of five of Jordan and Evermann's and Gilbert's specimens has shown nothing to separate them specifically from the specimens of **fernandinus* which we have seen from the offing of South Carolina, from the Gulf of Mexico, from the Mediterranean, and from Juan Fernandez (type locality), whether in relative positions of fins, in bodily proportions, or in the shape of the denticles on the sides of the body.

**S. fernandinus* has also been reported from the Philippines under its own name (with brief description) by Herre (1923, p. 73; 1934, p. 12); also as *philippinus* Smith and Radcliffe (1912, p. 677, Pl. 51, fig. 1), a supposedly new species based, however, on a specimen that is not separable from *fernandinus* either in fin characters or in its denticles, as Mr. Stewart Springer informs us from a recent examination of it in the U. S. National Museum. We should note in passing that Whitley (1931, p. 310) had proposed a new name, *montalbani,* to replace *philippinus* Smith and Radcliffe, the latter name having long been preoccupied within

[8] On this point, see also Jordan and Hubbs 1925, pp. 105-106.

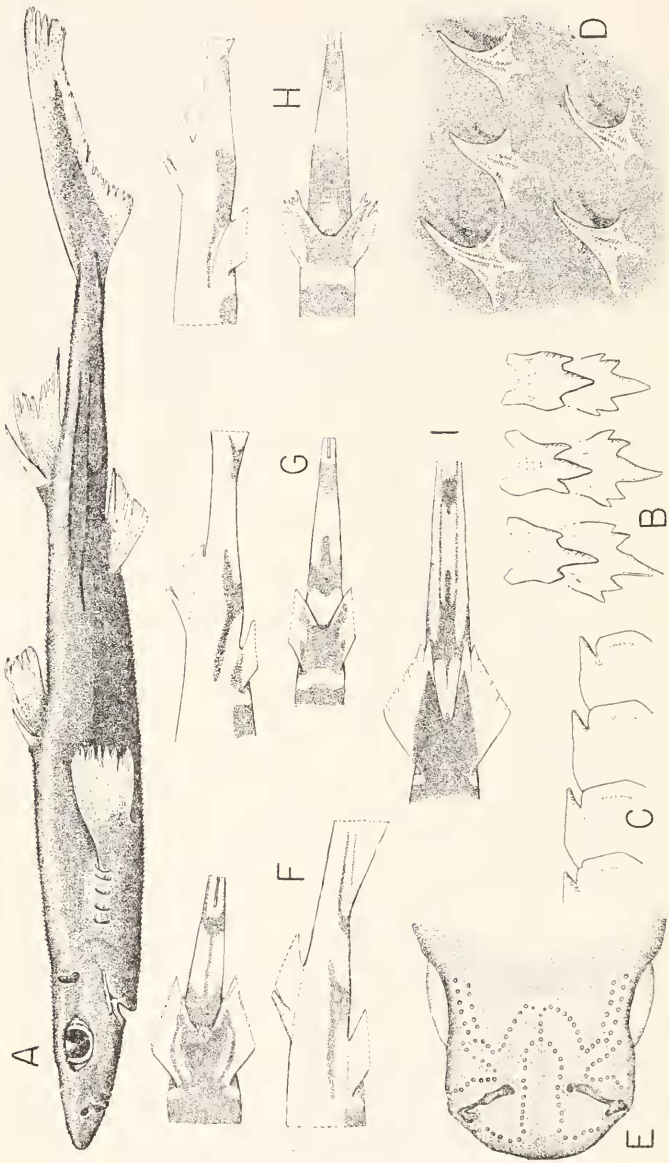

FIGURE 5

the genus *Squalus* by *philippinus* Shaw 1804 (p. 341), proposed for an Australian heterodontid. For details see Whitley.

**S. fernandinus,* to continue, has been reported from Mauritius, both as *blainvillei* (by Sauvage 1891, p. 11) and as *acutipinnis* (by Regan 1908, p. 47). It has long been known also in Australian waters, where it seems first to have been reported, with at least presumptive evidence of identity, by Günther (1870, p. 419) as *blainvillei,* and subsequently by that same name but without description by MacLeay (1881), by Ogilby (1889, p. 185), and by Lucas (1890, p. 44). A confusing feature here is that the only Australian report of a spiny dogfish under the name **fernandinus,* the identification of which was supported by a description or by an illustration (Waite 1921, p. 23, fig. 30), seems not to have been based on that species, but on the local representative of the *megalops* division of the genus.

Regan's (1908, p. 46) identification, however, of a spiny dogfish from Tasmania as **fernandinus* was no doubt correct, for we have found nothing to separate the type specimen of **tasmaniensis* Rivero 1936 (now in the Museum of Comparative Zoology) from our specimen of **fernandinus* from the type locality of the species (Juan Fernandez). For an extensive list of Indo-Pacific records for *fernandinus* see Herre 1953, p. 31.

With the evidence of widespread occurrence so conclusive for *fernandinus* for the Australian region in general, it seems astonishing that there has been no report yet for New Zealand waters of a spiny dogfish, the accompanying account of which places it definitely in **fernandinus.* In fact, the only report under that name of a New Zealand *Squalus* that includes any clear evi-

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Fig. 5, A, *Etmopterus bullisi,* new species, juvenile male, 230 mm. long (U. S. Nat. Mus. No. 158186), off northeastern Florida. B, upper teeth of same, x about 9. C, lower teeth of same x about 12. D, dermal denticles of same, from side below first dorsal fin, x about 30. E, *Etmopterus polli,* immature male about 226 mm. long, off south equatorial West Africa, Mus. Comp. Zool. No. 38000, lower surface of anterior part of head, x about 1.4. F, *Etmopterus spinax,* Norway, to show black pattern on posterior part of trunk. G, corresponding drawings of *E. virens,* northern part of Gulf of Mexico. H, corresponding drawings of *E. hillianus,* north coast of Cuba; F-H, x about 0.4, after Bigelow, Schroeder and Springer 1953, Fig. 6. I, corresponding drawing of *E. abernathyi,* type specimen, x about 0.4, after Garrick 1957, Fig. 3C.

dence of specific identity (Waite 1909, p. 142, Pl. 16, fig. 1; Phillipps 1928, p. 223, fig. 3) was evidently based on a member of the *acanthias* division. Thus the accompanying illustration shows its sides as white spotted, its first dorsal fin as originating posterior to the rear inner corner of the pectorals when the latter are laid back, and the mid-point of the bases of its pelvics as nearer to the origin of the second dorsal than to the rear end of the base of the first dorsal.

It is astonishing, also, that while **fernandinus* must be common around Juan Fernandez, to judge from the number of specimens that have found their way thence to various museums (Delfin 1901, p. 21), and is reported from northern Argentine waters, on the conclusive evidence of a small one found in the stomach of an albatross (Lahille 1928, p. 327, fig. 17), we have found no positive report of its presence in continental waters along the coast of Chile. Thus Philippi's (1887, p. 27) inclusion of it (under the name *firmandezianus*) in his account of the sharks of Chile seemingly harked back to Molina's original report of it from Juan Fernandez. Neither does Delfin (1901) mention any Chilean localities for it other than Juan Fernandez, which is some 240 miles off the Chilean coastline; nor does Fowler's (1930, p. 495) nominal reference of it to "Chile" include any continental locality. Neither has it been reported from Peru, nor from the Pacific coast of Central or North America, for that matter.

Megalops division. The earliest adequate account (with illustration) of a representative of this was by McCulloch (1927, p. 9, Pl. 2, fig. 25a; illustration later copied by Whitley 1940, p. 138, fig. 147) of an Australian shark that was identified by him as **megalops* MacLeay 1881. And Dr. Whitley writes us that he has verified this identification, by comparison with the type specimen of **megalops*, which he has had the kindness to examine at our request. The accompanying illustration (Fig. 4B) reproduces a tracing of its pectoral fin which Dr. Whitley has kindly sent us. We are also fortunate enough to have at hand three excellent specimens of **megalops*, 526-550 mm. long, from New South Wales, for which the Museum is indebted to Col. John K. Howard.

The Japanese *brevirostris*, described and beautifully pictured by Tanaka (1917, p. 464, Pl. 129, figs. 362, 363; Pl. 130, fig. 364)

resembles **melagops* so closely that we have no doubt a comparison of specimens from the two regions would lead to their union as **megalops,* this being the older of the two names.

The **megalops* division is represented in the Atlantic by **cubensis* Rivero 1936, which is known from Cuban waters (type region), from the northwestern part of the Gulf of Mexico, (specimen recently taken by "Oregon" and referred to us by Mr. Stewart Springer), probably Trinidad and from Rio de Janeiro, whence it was reported by Ribeiro (1907, p. 168) under the name *blainvillei* (Bigelow and Schroeder 1948, p. 478, footnote 63).

**S. cubensis* closely resembles **S. megalops* in proportional dimensions, and in the shape of the denticles on the sides of its body (Fig. 3), but differs in a relatively longer first dorsal fin spine, in somewhat differently shaped caudal and pectoral fins (Fig. 4), and in the location (relative to the dorsal fins) of the pelvic fins, the midpoint of the bases of which are about midway between the rear end of the base of the first dorsal and the origin of the second dorsal in **cubensis* (a little nearer to the rear end of the base of the first dorsal than to the origin of the second dorsal in **megalops*). No representative of this division of the genus has yet been reported from the eastern side of the Atlantic, or from the Mediterranean.

Genus CIRRHIGALEUS Tanaka 1912

Cirrhigaleus Tanaka 1912, type species *C. barbifer* Tanaka 1912b, p. 151, Pl. 41, figs. 156-162; Japan.

Generic synonym:

Phaenopogon Herre 1935, type species *P. barbulifer* Herre 1935, p. 123, fig. 1; Japan.

Generic characters. In general as in *Squalus* (p. 26), but without precaudal pit either above or below; posterior part of trunk without longitudinal ridges; and anterior margin of nostril, near inner end, with a well developed and very conspicuous fleshy barbel tapering to a slender tip (a feature unique among squaloid sharks); dermal denticles on sides of body with tridentate rear margins, their outer surface with three corresponding ridges. Also, in the only species that has yet been seen, the back is more highly arched than it is in any known *Squalus,* and

the body is subtriangular in cross section. Maximum recorded length 855 mm.

Remarks. Garman (1913, p. 457), followed by Fowler (1941, pp. 255, 275) reduced *Cirrhigaleus* to a subgenus of *Squalus* in rank. But the presence of the nasal barbel, combined with the lack of precaudal pits and of longitudinal-lateral ridges on the caudal peduncle seem fully to justify its retention as a distinct genus. *Phaenopogon* Herre, proposed without mention of Tanaka's (1912) earlier account of *Cirrhigaleus,* is clearly equivalent to the latter, to the synonymy of which Herre himself (1936, p. 59) has already relegated it.

Species. One species only is known, *C. barbifer* Tanaka 1912, which was based on a single male, 855 mm. long, from the Tokyo market. A second specimen (a female of 555 mm.) from Misaki, Japan, has more recently been described and pictured by Herre (1935, p. 123, fig. 1) as *Phaenopogon barbulifer.*

Genus CENTROSCYLLIUM Müller and Henle 1841

Centroscyllium Müller and Henle 1841, p. 191. Type species **Spinax fabricii* Reinhardt 1825, West Greenland.

Generic synonym:

Paracentroscyllium Alcock 1889, p. 379, type species *P. ornatum* Alcock, Bay of Bengal.

Generic characters. Squalinae with upper teeth similar to lowers, erect and symmetrical, or nearly so, all along the jaw; the teeth in both jaws with 3-5 cusps, the median cusp much the largest; dorsal fin spines well developed, with two longitudinal grooves on either side; lower posterior margin of caudal fin with subterminal notch (but see discussion, p. 46); caudal peduncle without precaudal notch either above or below, and without lateral-longitudinal ridges; inner corner of pectoral fins rounded in known species; snout in front of mouth not more than one-half as long as head to origin of pectoral fins; preoral clefts present, slightly expanded inwardly; dermal denticles thorn-like, on stellate bases; newborn specimens naked, the denticles developing first along the back, spreading later to sides, and subsequently to the lower surface (see further, p. 41); some species, at least, with thickenings of the skin that presumably are luminous. Maximum recorded length 829 mm., for *C. fabricii.*

Depth range. The only member of this genus for which we have more than scattered records (*fabricii,* p. 41) seldom (if ever) has been taken shoaler than 275 meters; its center of abundance lies deeper than about 500 meters. It is known to occur down at least to 1100 meters, and there is a somewhat questionable report of it from about 1495 meters (for details see Bigelow and Schroeder, 1948, p. 485). Depth records for other members of the genus have been from between 448 and 1024 meters.

Remarks. The few known species that fall in *Centroscyllium* as generally defined are set apart from all other known members of the subfamily Squalinae by their dentition, the teeth having 3-5 cusps in both jaws. In this respect they are approached the most nearly by *Etmopterus,* in which the uppers have 3-7 cusps, but the lowers have only one. In all other known members of the subfamily the teeth (uppers as well as lowers) have only one cusp.

The genus *Paracentroscyllium* was proposed by Alcock (1889, p. 379) for three juvenile sharks, 5¼ inches long, from the Bay of Bengal, allied to *Centroscyllium* except that they had "monocuspid teeth" and an "absolutely smooth integument." But the nakedness of the skin was clearly a juvenile character (this accords with conditions in **fabricii,* see p. 41); and the lateral cusps on the teeth seem merely to have escaped notice, for Alcock's (1896, p. 308) subsequent study of four additional specimens up to nearly one foot long from the Arabian Sea led him to emend his original diagnosis of *ornatum* to read "minute tricuspid teeth in both jaws" and body "covered with minute placoid deciduous scales." Accordingly, in 1896 (pp. 308, 310) he united *Paracentroscyllium* with *Centroscyllium.* Hence it was as a *Centroscyllium* that he pictured *ornatum* in 1900 (Pl. 35, figs. 1-1B, including a figure of one of its denticles). And Fowler's (1941, p. 252) revival of *Paracentroscyllium,* as a subgenus of *Centroscyllium,* for species in which the "caudal ends in point posteriorly, lower edge of fin without distinct posterior notch," (harking back, no doubt, to Regan's [1908, p. 40] key to the species of *Centroscyllium*), runs counter to Burkhardt's (1900, p. 567, fig. 8) illustration of one of Alcock's original specimens, for this shows the caudal as blunt-tipped and with a distinct (though shallow) subterminal notch.

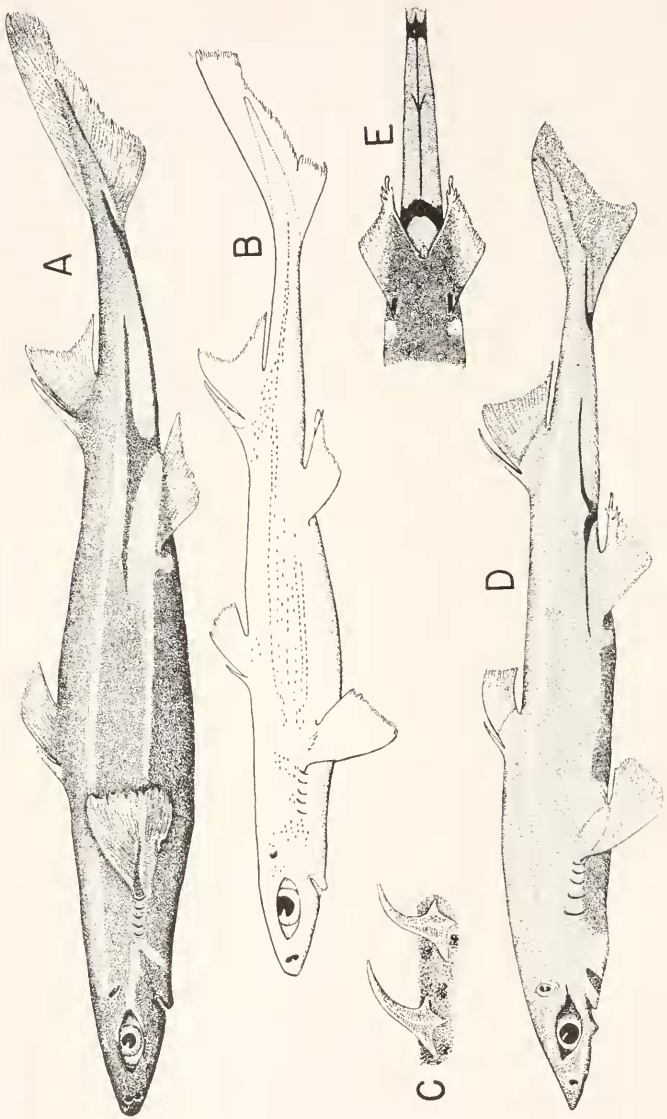

FIGURE 6

Species. The following supposedly separate species fall in *Centroscyllium*: **fabricii* Reinhardt 1825 (type species), both sides of the northern Atlantic; *granulatum* Günther 1887, Falkland Islands; *ornatum* Alcock 1889, Bay of Bengal and Arabian Gulf; **nigrum* Garman 1899 (incl. **ruscosum* Gilbert 1905), eastern Pacific off Panama (vicinity of the Galapagos, vicinity of Cocos Island), also Hawaiian region; and **ritteri* Jordan and Fowler 1903, Japan.

**C. fabricii,* the common "black dogfish" of English-speaking North Atlantic fishermen, has been described by several authors. Even so, examination of large catches made recently off the Nova Scotian coast (Bigelow and Schroeder 1954, p. 40) enables us to expand our earlier account (Bigelow and Schroeder 1948, p. 482) in the following respects. The teeth are already tricuspid in both jaws on specimens not more than 165 mm. long (suggesting that this is already the case at the time of birth), and the skin, then, is wholly naked above as well as below, just as Alcock (1889, p. 379) described it for the original (133 mm.) specimens of his *ornatum* from the Bay of Bengal. But a **fabricii* of 171 mm. already shows a dense band of denticles along the back, with a few on the upper part of the sides below the second dorsal fin. On one of 177 mm., the back as a whole, and the sides above the mid-level are rough with denticles, though the lower surface still is smooth. And the situation is much the same on one of 273 mm. But on specimens of 300 mm. and larger, the belly, like the upper parts, is strewn with denticles.

The color pattern, too, undergoes an interesting alteration with growth. The smallest specimen we have seen (165 mm. long) is ink-black below and slightly paler along the back and on the basal parts of the fins, with the two dorsals and the pectorals margined and the pelvics tipped with white, and with

Fig. 6. A, *Etmopterus lucifer,* female 337 mm. long, Japan, Mus. Comp. Zool. No. 1109. B, outlines of juvenile male, 267 mm. long, Japan, Mus. Comp. Zool. No. 1123, to show the distribution of the black, presumably luminescent, markings. C, denticles from side of body below first dorsal fin of specimen shown in A, x about 35. D, *Etmopterus brachyurus,* male, 300 mm. long, Japan, after Smith and Radcliffe with the black markings added from the type specimen in the U. S. National Museum. E, ventral view of posterior part of trunk of same specimen.

white fin spines. The development of the denticles (see above) is accompanied by a paling to deep chocolate brown, first along the mid-zone of the back, then along the upper part of the sides, as illustrated by specimens of 171-177mm. (see above). The belly, however, continues black and the fins continue white-edged up to a length of 200-225 mm. But it is only the extreme tips of the dorsal fins that show any trace of white by the time a length of 280-330 mm. is reached, and all the fins on larger specimens are uniformly blackish right out to the margins. Meantime, the back and the upper part of the sides darken again after the dermal denticles have spread to the lower surface, so that half-grown specimens, and larger, are black above as well as below when taken from the water, unless the skin has been rubbed off, as often happens in the trawl. We have seen no exception to this rule among the many specimens we have handled during the cruises of "Caryn" and of "Capn. Bill II" during 1949, 1952 and 1953 (Bigelow and Schroeder 1954, p. 41). Our earlier account of the color of adult **fabricii* as "deep chocolate brown, darkest (almost black) below and on the fins generally" (Bigelow and Schroeder 1948, p. 485) was based on a specimen that had reposed for several years in alcohol.

We think it evident, from the foregoing, that changes with growth must be taken into account in any discussion of the possible taxonomic significance of fin-markings and of the regional distribution of dermal denticles in this particular genus.

The North Atlantic, Japanese, and Falkland Island representatives of the genus all seem to deserve continued recognition as separate species, though they resemble one another closely in general appearance. Thus the distance from the upper origin of the caudal fin to the rear end of the base of the second dorsal fin is as long as from the eye to the level of the 4th-5th gill openings in **ritteri* of which we have an excellent specimen at hand, about 425 mm. long (Fig. 7A), whereas in **fabricii* of about that same size the caudal peduncle (measured as above) is only about as long as from the eye to the first gill openings. This contrast, indeed, was invoked as alternative between the Japanese and North Atlantic populations in our earlier key to the species of *Centroscyllium* (Bigelow and Schroeder 1948, p. 482). The denticles, too, on specimens of about equal sizes are somewhat sparser on **ritteri* than on **fabricii;* as an illustration,

7 or 8 denticles on the side, below the first dorsal fin, counted along a nearly straight line, occupy a length of 1 cm. on our **ritteri* of 425 mm., but 8 to 12 denticles occupy this space on the specimens of **fabricii* of about 400 mm.

The general coloration of the body seems also to be distinctive here, for all the **fabricii* we have handled, large enough for the denticles to have spread to the lower surface (p. 41), have been plain above as well as below, not only when fresh but after a few years' stay in alcohol. But the two original specimens of **ritteri*, taken three years previous, are described as "uniform dark grayish brown, blackish below in front" (Jordan and Fowler, 1903, p. 635). And this applies equally to the alcoholic specimen of **ritteri* we have at hand, the lower surface of which is densely denticulate, while it also shows a definite black flank mark on either side of the rearward part of the trunk (Fig. 7A).

Judging from Burkhardt's (1900, p. 567, fig. 7) outline drawing of the type specimen (270 mm. long), *C. granulatum* Günther 1887, from the Falkland Islands, agrees more closely with **ritteri* than with **fabricii* in the length of the caudal peduncle relative to the dimensions of the head. But Günther's (1887, p. 7) characterization of the dermal denticles of *granulatum* as "much coarser" than those of **fabricii* "and in the form of granulations" sets it apart equally from **ritteri*, the thorn-like denticles of which (Fig. 7C) more nearly recall those of **fabricii* (Bigelow and Schroeder 1948, fig. 91), except that they are relatively somewhat longer and more slender.

With **ritteri* clearly separable from **fabricii*, and *granulatum* seemingly so, the same might have been expected to hold good for **nigrum* (including **ruscosum* Gilbert 1905) ; or at the least, a closer relationship might have been expected with **ritteri* than with **fabricii* on geographic grounds. Actually, however, **nigrum* is pictured both by Garman (1899, Pl. 1, fig. 2) and by Beebe and Tee Van (1941, p. 120, fig. 32), as falling with **fabricii* in the shortness of its caudal peduncle relative to the dimensions of the head, which we can corroborate from our examination of one of Gilbert's original Hawaiian specimens of his **ruscosum*, about 400 mm. long (the co-type), loaned us by the Stanford University Museum through the kind offices of Dr.

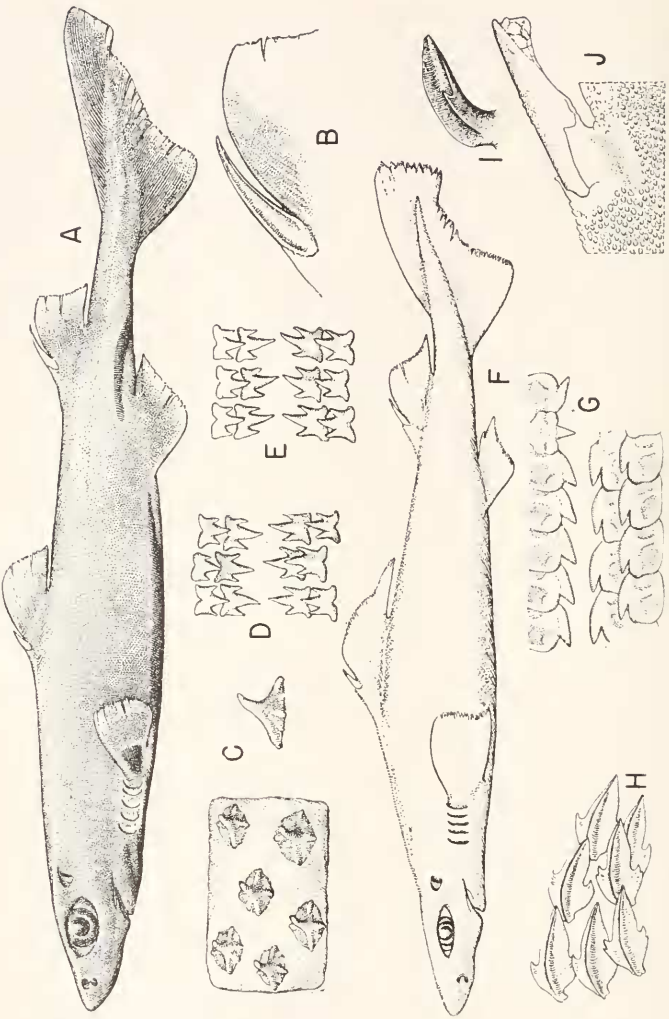

FIGURE 7.

George Myers,[9] and of the type specimen in the U. S. National Museum. Nor can we find anything in the dermal denticles to separate **nigrum* from **fabricii.*

Also, Garman's (1913, p. 230) use of the number of cusps on the lower teeth as alternative between **nigrum* (with five) and **fabricii* (with three) has failed to withstand the test of time, for most of the lowers midway along either side of the jaw actually have five cusps in **fabricii* (Bigelow and Schroeder 1948, p. 483, fig. 91E). And Beebe and Tee Van (1941, p. 121) have found that on their Cocos Island specimens of **nigrum* the outermost pair of cusps were not as prominent as pictured by Garman (1899, Pl. 4, fig. 6).

**C. nigrum,* however, maturing at a length of only about 400 mm. (Gilbert 1905, p. 581) or perhaps smaller still (Beebe and Tee Van 1941, p. 120) is a much smaller shark than **fabricii,* the males of which seemingly do not mature until at least 600 mm. long. Also, the pectoral and dorsal fins continue white tipped to maturity in **nigrum* (Gilbert 1905, p. 581, fig. 230; Beebe and Tee Van 1941, p. 120, fig. 32) though with the white areas somewhat reduced, whereas half-grown specimens of **fabricii,* and larger, show no trace of the white fin-markings that are so conspicuous on small specimens (p. 42). It may also prove (when more specimens have been examined) that it is characteristic for the pectorals to extend somewhat farther rearward in **nigrum* than in **fabricii,* for they are pictured both by

[9] The larger of Garman's original two specimens of **nigrum,* used as the basis for his account of the anatomy of the genus *Centroscyllium,* is now in a very fragmentary condition.

Fig. 7. A, *Centroscyllium ritteri,* female about 425 mm. long, Mus. Comp. Zool. No. 1370. B, second dorsal fin spine of same drawn to larger scale to show the longitudinal grooving. C, dermal denticles from side below first dorsal fin, x about 6 to 8. D, upper and lower teeth from central part of jaw, x about 4. E, upper and lower teeth from midway along side of jaw, x about 4. F, *Centrophorus foliaceus,* immature male, 351 mm. long, in U. S. Nat. Mus., from Japan. G, upper and lower teeth of same at center of mouth, x about 4. H, denticles of same from side below first dorsal fin, x about 13. I, lateral view of denticle, x about 18. J, *Centrophorus armatus,* southern Africa, second dorsal spine of specimen 330 mm. long, x about 3.5, from a photograph kindly contributed by Dr. J. L. B. Smith (see p. 6).

Garman (1899, Pl. 1, fig. 2) and by Beebe and Tee Van (1941, p. 120, fig. 32) as reaching nearly or quite to a perpendicular at the point of emergence (from the skin) of the first dorsal spine, which is true also of the Hawaiian specimen we have seen (mentioned above). It therefore seems justifiable to accept **nigrum* as a distinct species, at least until a larger number of specimens from the Pacific populations have been studied with a critical eye.

C. ornatum of the northern Indian Ocean falls with the *fabricii-nigrum-ritteri* group in its thorn-like denticles (Alcock 1900, Pl. 35, fig. 1). It agrees more nearly in proportional dimensions with **nigrum* of low latitudes in the eastern Pacific than with **ritteri* of the northwestern Pacific, the distance from the rear end of the base of its second dorsal fin to the origin of the upper side of its caudal fin being only about as long as from the eye to the first pair of gill openings, while its pectorals reach rearward about to a perpendicular at the point of emergence of the first dorsal fin spine. But Alcock (1896, p. 308) describes the fins as well as the trunk as "uniform jet black" on specimens nearly one foot long. Neither does his account of the type specimen, 133 mm. long, nor his illustration of it (Alcock 1894, Pl. 8, fig. 2) suggest any white fin-markings, such as are conspicuous on *nigrum* to maturity. While Regan (1908, pp. 40-41) characterized *ornatum* as without a distinct posterior notch on the caudal fin, seemingly following Alcock's (1894, Pl. 8, fig. 2) original illustration, Burkhardt's (1900, p. 567, fig. 6) drawing of one of the original series in the British Museum clearly indicates a subterminal notch. And Alcock's (1900, Pl. 35, fig. 1) second representation of the caudal of a larger specimen seems more fanciful than realistic, so widely does it differ from his earlier illustrations. With our knowledge of *ornatum* so far from adequate, and with the specimens of it in the collection of the Zoological Survey of India in a bad state of preservation (the late Dr. S. L. Hora has so written us in a recent letter), a final decision as to its status obviously is a matter for some future student. Meanwhile we believe a tentative key to the species of *Centroscyllium,* using the length of the caudal peduncle as the first alternative, seems likely to be more helpful for identification than our earlier key, in which the primary alternative is the location of the rear margin of the pectoral fin (when laid back) relative to the location of the first dorsal fin spine.

Provisional Key to Species of *Centroscyllium*

1. Distance from rear end of base of second dorsal fin to origin of upper side of caudal fin nearly or quite as long as from eye to level of origin of pectoral fins .....**ritteri* Jordan and Fowler 1903
Japan (Fig. 7 A,B,C). p. 42

Distance from rear end of base of second dorsal fin to origin of upper side of caudal fin only about as long as from eye to first-second gill openings 2

2. Dermal denticles on anterior part of trunk "in the form of granulations" (Günther 1887, p. 7) ..... *granulatum* Günther 1887
Falkland Islands. p. 43

Dermal denticles in the form of spines or thorns on stellate bases 3

3. Margin of pectorals, when laid back, falls short of a perpendicular at point of emergence from skin of first dorsal spine by a distance at least 25 per cent as long as eye .....**fabricii* Reinhardt 1825.
North Atlantic. p. 41

Margin of pectorals, when laid back, reaches nearly or quite to below point of emergence from skin of first dorsal spine 4

4. Dorsal, pectoral and pelvic fins white edged at all stages in growth
**nigrum* Garman 1899
(incl. *ruscosum* Gilbert 1905), eastern tropical Pacific off Central America, also Hawaiian region. p. 43.

Fins, as well as body, black at all stages in growth .....
ornatum Alcock 1889
Bay of Bengal and Arabian Gulf. p. 46

Genus ETMOPTERUS Rafinesque 1810

Etmopterus Rafinesque 1810, p. 14; type species *E. aculeatus* Rafinesque, Mediterranean, equals **Squalus spinax* Linnaeus 1758. Generic synonyms, see Bigelow and Schroeder 1948, p. 487.

Generic characters. Essentially as in *Centroscyllium* (p. 38), except with lower teeth much as in *Squalus*, i.e., much broader than the uppers and with only one cusp, the base of each tooth overlapping that of the next outward so that each row forms a continuous dental band, and with the cusps directed so strongly outward all along the jaw that their successive inner margins act as a nearly unbroken cutting edge (Bigelow, Schroeder and Springer 1953, figs. 7-10); dermal denticles on sides of body

ranging from thorn-like to bristle-like and to truncate, on quadrate bases.

Size. At maturity the various species of *Etmopterus* range in length from slightly more than 200 mm. (**virens,* perhaps also **villosus*) to a recorded maximum of 728 mm. in the case of **princeps* (Collett 1904, p. 4).

Depth range. The members of this genus are creatures of at least moderately deep water, where (as a group) their depth range is a wide one. The shoalest captures we find recorded for any of them are 73-91 meters for **spinax* in the northernmost parts of its range (Smitt 1895, p. 1165) and 183 meters for **abernathyi*, off New Zealand (Garrick 1957, p. 181); the deepest are 2074 meters for *E. princeps* (see Bigelow, Schroeder and Springer 1953, p. 251; Bigelow and Schroeder 1954, p. 47; and Grey 1956, p. 95 for details as to **princeps*). Most of the records for one species or another in various parts of the world have been from about 300 meters to about 900-1000 meters.

Remarks. These small, black-bellied deep-water sharks, of which some 16 recognizably distinct species are known, form a very compact unit. Characters that have proved the most useful for diagnosis of species within the genus are: the sizes and relative positions of the fins; the color pattern, whether uniformly as dark above as below or paler above with conspicuous dark flank markings of characteristic shape, whether or not with complex patterns of longitudinal bands of black dashes and dots (presumably luminescent) and whether with or not with white fin markings; also, for half-grown specimens and larger, the shapes of the dermal denticles, and their arrangement. But in using the denticles for diagnosis allowance must be made for the size of the specimens in question, for we have found that in one species (**princeps*) where the denticles are bristle-like on very young specimens, they are succeeded by thorn-like forms on half-grown individuals and larger (Fig. 3, F, G).

For accounts of the luminescent organs (for the species that have them) and of luminosity in this genus, see Johann (1899) and Oshima (1911).

Whitley (1939, p. 266) has revived the genus *Acanthidium* Lowe 1839, type species **A. pusillum* Lowe 1839 (=*Centrina nigra* Lowe 1834, preoccupied), designated by Jordan and Evermann (1896, p. 55), as distinct from *Etmopterus* Rafinesque

1810, type species *E. aculeatus* Rafinesque, (=**Squalus spinax* Linnaeus 1758). And Fowler (1941, p. 251) has recognized two corresponding subgenera within the genus *Etmopterus,* namely *Acanthidium* Lowe 1839, with "second dorsal origin behind ventral base; first dorsal origin midway between orbit and second dorsal origin," and *Etmopterus* Rafinesque 1810 with "second dorsal origin over or a little before ventral base; ventral origin slightly nearer subcaudal origin than pectoral origin." But these differences do not seem to us wide enough for generic — or even subgeneric — separation (p. 22; Bigelow, Schroeder and Springer 1953, p. 238). *Acanthidium* as employed by Garman (1913, p. 215) in a different sense, is discussed on p. 21.

Species. The genus *Etmopterus* is especially interesting from the taxonomic standpoint, because it is already known to include a larger number of recognizable species than we have any reason to suppose is included in any other genus of squaloid sharks. These species, it is true, resemble one another so closely in general aspect that any one of them might easily be mistaken for any other, on cursory inspection. But closer examination has shown that they are sharply separated by differences both in the relative positions of the fins and in the nature and arrangement of the dermal denticles, and also in the color pattern which has proved a much more convenient species-character here than it is usually thought to be among other sharks.

The following seven species have been known from the North and Equatorial Atlantic, including the Mediterranean and the Gulf of Mexico.

1. **spinax* Linnaeus 1758, type species of the genus (many of the reports of it have been as *niger* Cloquet 1820, p. 93); eastern North Atlantic (including the Mediterranean) from the Cape Verde Islands, Morocco and the Azores to Norway.

2. **pusillus* Lowe 1839 (=*Centrina nigra* Lowe 1834, but *nigra* is preoccupied in *Etmopterus* by *niger* Cloquet 1820, proposed in substitution for *spinax* Linnaeus 1758 and employed by many subsequent authors); tropical-subtropical Atlantic, from tropical West Africa to the Canaries, Madeira, and the Azores in the east (including the Mediterranean) and Gulf of Mexico in the west, where it has been found recently (Bigelow, Schroeder and Springer 1955, p. 2). The Japanese shark described and pictured under the name *pusillus* by Tanaka (1912,

Pl. 22; 1912[a], p. 88) was based on a clearly separable form (see below, p. 58).

3. **hillianus* Poey 1861, Cuban-West Indian region, northward to the offing of Chesapeake Bay.

4. **princeps* Collett 1904, both sides of the North Atlantic, Faroes-Hebrides region and offing of Gibraltar in the east; continental slope in the west where it is common from the offing of southern Nova Scotia to that of southern New England (Bigelow and Schroeder 1954, p. 46).

5. **polli* Bigelow, Schroeder and Springer 1953, equatorial West Africa.

6. **schultzi* Bigelow, Schroeder and Springer 1953, northern part of the Gulf of Mexico.

7. **virens* Bigelow, Schroeder and Springer 1953, northern part of the Gulf of Mexico.

For the diagnostic characters of the members of this group, see Bigelow, Schroeder and Springer 1953, p. 237.

An eighth North Atlantic *Etmopterus*, from the east coast of Florida, is described here as a new species, **E. bullisi*.

Etmopterus bullisi n. sp.

Figure 5 A-D

Plate 2

Type specimen. Female, 196 mm. long; "Pelican" Sta. 42, off northeast coast of Florida, Lat. 30°02′ N, Long. 80°05′ W; 205 fathoms (U. S. Nat. Mus. No. 158186).

Additional material: female of 205 mm. and immature male of 230 mm. from this same locality; also immature male of 212 mm., "Pelican" Sta. 51, off eastern Florida, Lat. 29°48′ N, Long. 80°09′ W, about 200 fathoms.

Description. Proportional dimensions in per cent of total length of type specimen, and of a male 230 mm. long, to nearest 0.1 per cent.

Snout length in front of: outer nostrils 2.5, 2.8; mouth 11.7, 12.2.

Eye: horizontal diameter 4.6, 4.6.

Mouth: breadth 7.1, 7.0.

Nostrils: distance between inner ends 2.8, 2.8.

Gill openings: lengths first 2.3, 1.7; third 2.3, 1.7; fifth 2.0, 1.5.

First dorsal fin: vertical height 3.1, 2.8; length of base 4.6, 4.4.
Second dorsal fin: vertical height 4.6, 4.4; length of base 7.4, 7.0
Caudal fin: upper margin 24.0, 23.5.
Pectoral fin: outer margin 11.0, 10.0; inner margin 4.8, 5.6, width 4.6, 5.2.
Distance from snout to: 1st dorsal 33.7, 33.0; 2nd dorsal 56.6, 57.9; upper caudal 76.0, 76.5; pectorals 25.0, 24.4; pelvics 51.5, 50.0.
Interspace between: First and second dorsals 18.3, 18.7; 2nd dorsal and caudal 12.7, 13.9; base of pelvics and caudal 18.9, 20.4.

Teeth: $\frac{20\ 18}{27,\ 31}$, —

Description of type specimen. Trunk noticeably slender, its height at pectorals (where highest) about 12 per cent as great as its length to upper origin of caudal fin, its greatest thickness about equal to its greatest height; body narrowing rearward with caudal peduncle nearly as thick as high. Head flattened above, its length to origin of pectorals occupying about 33 per cent of trunk to origin of caudal fin.

Snout obtusely wedge-shaped anteriorly, its length in front of mouth about 50 per cent as great as length of head to origin of pectorals, its length in front of eyes about 28 per cent. Eye about 1.4 times as long as high, its horizontal diameter about 40 per cent as long as snout to mouth. Nostril with outer end close to edge of snout; anterior narial flap triangular, with pointed tip, reaching across narial opening. Pores on lower surface of snout so small that they are visible only on close scrutiny. Mouth low-arched, occupying about 80 per cent of breadth of head. Preoral clefts short, extending about 33 per cent the distance from corners of mouth toward nostrils. Furrows from corners of mouth reaching rearward half way toward first gill openings.

First gill openings a little shorter than distance between nostrils; fifth openings a little shorter than first to fourth; anterior margins only slightly concave, but tips of filaments exposed in first to third. Teeth smooth edged as in other members of this genus; uppers with only 3 cusps, the axial much the largest. Lowers with cutting edge nearly parallel with general trend of the jaw. Cusp of the median lower tooth, identified as such by its base overlapping that of the next tooth on either side, directed strongly outward, to the one side or the other, on all specimens seen. Two or three rows functional in upper jaw but one row only in lower jaw.

Dermal denticles low, conical-thorn-like, erect or nearly so and so sharp that the skin feels very rough. Denticles on lower surface straight, or nearly so, in random arrangement, but those on sides and back slightly curved rearward and arranged in single series in regular longitudinal rows (Pl. 2); the rows on the back anterior to the first dorsal fin converging rearward, but the rows on the sides paralleling in general the main axis of the trunk as far rearward as abreast the second dorsal, whence those above the mid-level trend downward-rearward along the tail sector and out along the caudal axis. The lower surface of the trunk, like sides and back, is closely set with denticles, except for the chin, the lips, a small area in the midline of the snout close in front of the mouth, and the margins of the nostrils, which are naked. Fins as a whole naked.

Base of first dorsal fin about as long as eye, its origin posterior to the origin of the pectorals by a distance about as long as from tip of snout to mouth. Rear end of base of first dorsal about equidistant between perpendiculars at axil of pectorals and at origin of pelvics. Distance from point of emergence from skin of first dorsal spine to point of emergence of second dorsal spine about as long as head to origin of pectorals. Second dorsal spine about 1.8 times as long as first, each measured from point of emergence from the skin, its tip reaching about 75 per cent toward the upper corner of the fin. Distance from rear end of base of second dorsal fin to origin of upper side of caudal fin about 54 per cent as long as between points of emergence from skin of first and second spines, and about 47 per cent as long as length of head to pectorals; upper side of caudal fin about as long as head to origin of pectorals, its shape as pictured in Figure 5A. Lower anterior margin of caudal 43 per cent as long as upper margin. Distance from origin of lower side of caudal fin to rear end of bases of pelvics about 75 per cent as long as head to origin of pectorals. Rear end of bases of pelvics a little anterior to point of emergence, from skin, of second dorsal spine. Pectorals truncate, with rounded corners, the distal margin, when laid back, falling about abreast of point of emergence from skin of first dorsal spine.

In their present state the edges of the pectorals, dorsals, and pelvics, and the terminal sector of the caudal, are much frayed out on all the specimens. But close examination makes it evident

that, normally, they are entire, not fringed as they are on **E. schultzi* (Bigelow, Schroeder, and Springer, 1953, p. 254, Fig. 9D).

Claspers of mature males not yet seen.

Color. Upper parts in general very dark sooty gray, the midline of the back paler (as a definite band on one of the specimens), with a vaguely outlined pale yellowish spot on the top of the head between the eyes. Lower surface of head and body sectors black; the black extending rearward in a narrow band along the lower surface of the tail sector, nearly or quite as far as the origin of the caudal; also upward on each side close behind the pelvics, to continue forward as a flank mark of the shape shown on Figure 5A. The pattern of coloration, however, is evident only on close examination, the sides, as a whole, being very nearly as dark as the belly. Distal parts of the dorsal, pectoral and pelvic fins, and lower edge of caudal pale gray after preservation, perhaps whitish in life.

The (presumably) luminescent system of markings to be seen on various other members of *Etmopterus* is evident here only as a row of black dots along the midline of the back from nape to base of caudal. If similar markings are present elsewhere they are masked by the dark hue and dense pigmentation of the sides.

Size. The size at maturity is not yet known.

Geographic range. So far known only off the northeast coast of Florida, at the localities listed above (p. 50).

Remarks. The linear arrangement of the denticles on its back and sides marks **bullisi* off from all the other species of *Etmopterus* that were known previously from the North Atlantic and Gulf of Mexico. It differs further from **spinax* in its stouter, thorn-like denticles, and in that the interspace between its first and second dorsal fins is only about as long as from tip of snout to first gill openings (as long as from tip of snout to origin of pectorals in **spinax*); from **hillianus* and from **virens* in its noticeably shorter caudal peduncle, relative to the length of the head; from **pusillus* in its thorn-shaped denticles (truncate with concave crown in **pusillus*); from **schultzi* both in the nature of the margins of its fins (p. 52) and in a relatively shorter caudal fin (upper margin only as long as from tip of snout to origin of pectorals in **bullisi*, but as long as from snout to rear edge of pectorals in **schultzi*); from **princeps* in a noticeably

longer interspace between its second dorsal and the origin of the upper side of its caudal (to mention only the most conspicuous difference); and from **polli* in its tricuspid upper teeth (mostly with 5 cusps in **polli*), in the roughness of the lower side of its snout, and in the minuteness of the pores there.

Among species known from other seas, it agrees with **lucifer* (originally described from Japan) in the linear arrangement of the denticles on the sides of the head and body, and in their thorn-like nature, also with **villosus* of Hawaiian waters; with **brachyurus*, originally described from the Philippines (p. 59); and with **abernathyi*, from New Zealand. But there is no danger of confusing it with either one of these for the following reasons: the distance from the tip of its snout to its first dorsal fin spine is shorter relatively than in **villosus* but its caudal fin is considerably longer; the upper margin of its caudal is much longer relatively than in **brachyurus;* the interspace between its two dorsal fins (not longer than from tip of snout to first gill openings) is noticeably shorter than in either **lucifer* or **abernathyi* (at least as long as from tip of snout to origin of pectorals), and its flank marks are much less conspicuous (cf. Fig. 5A with Fig. 6A) than in either of these last two.

The Mediterranean shark, also, that was named *Squalus infernus* by Blainville (1825, p. 59), a century and a quarter ago, is referable to *Etmopterus* by Blainville's account of its upper teeth as three-cusped, but of its lowers as one-cusped, with horizontal cutting edge.[10] And there is nothing in the dimensions given for it by Blainville to set it apart from **E. spinax,* as appears from the accompanying comparative table. Our earlier statement (Bigelow, Schroeder and Springer 1953, p. 224) that its proportional dimensions differ from those of other Atlantic species was based on a misreading of the measurements given for it by Blainville.

> Proportional dimensions in per cent of total length (A) for the type specimen, 255 mm. ("dix pouces") long, of *infernus* Blainville 1825; and (B) for a female **spinax,* about 285 mm. long, from the Mediterranean, in the Museum of Comparative Zoology.

[10] Notwithstanding its tooth characters, Garman (1913, p. 197) classed it as a synonym of **Centrophorus uyato* Rafinesque 1810. We may also point out that Blainville's (1825, p. 59) reference for it to his "Pl. 14, Fig. 2" was incorrect; actually this figure represents a **Lamna nasus.*

	A	B
Snout to 5th gill openings	19	21
Snout to cloaca	57	58
Snout to 1st dorsal fin	31	32
Snout to 2nd dorsal fin	63	63
Cloaca to lower origin of caudal fin	23	19

**S. spinax* has been reported from southern Africa as well as from the North Atlantic and Mediterranean, on the evidence of a shark that was taken off Cape Point by the "Pickle" (Gilchrist 1922, pp. 42, 49; Barnard 1925, p. 51; Smith 1949, p. 59), with two others taken in the same general region by the "Discovery" (Norman 1935, p. 37). And the "Pickle" specimen certainly falls with **spinax* in the relative positions of its fins, as well as in the bristle-like nature and irregular distribution of its dermal denticles, to judge from what little information is available. But we still await a detailed description of it (or of the specimens taken by "Discovery"); nor are the outlines of the black belly area and of the flank-markings shown on Smith's illustration. Final decision, in short, as to the specific relationship that the *spinax*-like form of South African waters bears to the typical **spinax* of the northeastern Atlantic must await a comparison of specimens from the two ocean areas. None of the other Atlantic species has been reported from farther southward in the southern hemisphere that latitude 6°08′S (*S. polli* Bigelow, Schroeder and Springer 1953, p. 241).

Other named sharks that can be definitely placed in *Etmopterus* are the following.

E. granulosus (Günther) 1880, originally reported from the southwest coast of South America, and subsequently from Argentina (Lahille 1921, p. 16, by name only) as well as from southern Africa (Gilchrist 1922, p. 41; Barnard 1925, p. 49; Smith 1949, p. 58). Barnard's reference of it to the Hawaiian Islands, without supporting date, may actually have referred to **E. villosus*. The chief diagnostic features of *granulosus* are: distance from tip of snout to emergence from skin of first dorsal spine is at least as long as from emergence of first dorsal spine to rear end of base of second dorsal (Günther 1880, Pl. 2, fig. C; Barnard 1927, Pl. 2, fig. 8; Smith 1949, p. 58, fig. 50); distance from rear end of base of pelvics to origin of lower side of caudal is shorter than from tip of snout to first gill openings;

margin of pectorals (when laid back) reaches nearly to abreast of base of first dorsal spine; dermal denticles on sides of body described as granular, without median spine and in irregular pattern, but those on tail in the form of minute spines and arranged in longitudinal bands (Günther 1880, p. 19); body uniformly dark brown to blackish, but the fins edged with white (Günther 1880, p. 19), a feature not mentioned either by Barnard or by Smith. Incidentally, the upper side of the caudal fin is shown as about as long as from the tip of the snout to the origin of the pectoral fins both by Günther (1880, Pl. 2, fig. C) and by Barnard (1927, Pl. 2, fig. 8), but only as long as from snout to first gill openings by Smith (1949, p. 58, fig. 50), a disagreement we cannot resolve.

**E. lucifer* Jordan and Snyder 1902, Japan (Fig. 6 A-C). The chief diagnostic features, as appear both from the original account and from our own examination of 5 specimens (two in the Museum of Comparative Zoology, three in the U. S. National Museum) are: distance from tip of snout to point of emergence from skin of first dorsal spine is about as long as from emergence of first dorsal spine to midpoint of base of second dorsal; upper side of caudal and distance from rear end of base of pelvics to origin of lower side of caudal both are about as long as from tip of snout to origin of pectorals; rear end of base of first dorsal is about midway between perpendiculars at origin of pelvics and at axil of pectorals; dermal denticles slender, thorn-like, weakly curved, sloping only slightly, and close set; those on the sides arranged in general in longitudinal rows and directed downward-rearward (a conspicuous feature), but those on the black areas of the lower surface in random pattern, directed obliquely downward-rearward on either side of the body toward the midline, where a single row is directed rearward. Upper surface of head, anterior to spiracles, with extensive naked areas. Back and upper part of sides chocolate brown; lower surface black, with a distinctive black marking on either flank (Fig. 6A; Bigelow, Schroeder and Springer 1953, fig. 6B), the line of transition from black to brown marked by a pale band as shown on Figure 6A. Imposed on the sides, there is also a complex pattern of black dash-like markings, presumably luminescent (Fig. 6B; Oshima 1911, pp. 1-3), in longitudinal linear arrangement.

Originally described from Japan, **lucifer* has since been found in South African waters (Gilchrist 1922, p. 49; Barnard 1925, p. 50; Norman 1935, p. 37; Smith 1949, p. 59, fig. 52). It has also been reported by name from the Philippines (Smith and Radcliffe 1912, p. 679, 21 specimens; Fowler 1941, p. 248). and from Flores Straits in the East Indies (Weber 1913, p. 597). But we think it more likely on geographic grounds that these reports from equatorial waters actually were based on **E. brachyurus* (p. 58).

**E. villosus* Gilbert 1905, from the Hawaiian Islands. The combination of slender, spine-like denticles (those on back and sides in linear series) with a first dorsal fin standing so far rearward that its point of origin is about midway between the tip of the snout and the origin of the upper side of the caudal fin (corroborated by our examination of the type specimen in the U. S. National Museum), sets **villosus* apart from all other members of the genus yet known. Other features diagnostic of **villosus* are: upper side of caudal about as long as from tip of snout to first-second gill openings; distance from rear end of pelvics to origin of lower side of caudal fin only a very little longer than from snout to level of spiracles; rear end of base of first dorsal about midway between origin of pelvics and rear margin of pectorals when the latter are laid back; abdomen and lower side of head blue-black, the sides brown, no black flank marks being suggested by Gilbert's (1905, Pl. 66) illustration or by our recent examination of the type specimen; dorsals, pectorals and pelvic fins broadly edged rearward with white; lower surface in general rough with denticles, the skin being naked only on the lips and nostrils, close around the eyes and spiracles, and close behind the dorsal, pectoral and pelvic fins, which are partially so; the denticles along the back and on the tail arranged in lengthwise series. On the type specimen, the denticles along the midline of the lower surface are smaller than they are pictured; the first dorsal spine is only about 65 per cent as long as the second; the upper teeth have only three cusps; and the cusps of the lower teeth are so strongly oblique that their inner margins are nearly parallel with the jaw.

**Villosus* is so far known only from the type specimen, 170 mm. long, taken by the "Albatross" off the south coast of Molokai (Gilbert 1905, p. 580, Pl. 66).

E. frontimaculatus Pietschmann 1907, from Japan. In general, this species resembles **E. lucifer* in color, with brown back and sides contrasting with ink-black belly and black flank marks. But the latter differ in shape from those of **lucifer,* as Oshima (1911, p. 2, fig. 1) has pointed out, while neither Pietschmann's account nor his illustration (1908, p. 657, Pl. 1, fig. 2) suggest the presence of the linear pattern of luminous organs to be seen on the sides of the body in **lucifer* (p. 56). *E. frontimaculatus* is set apart still more sharply from **lucifer* by its denticles, which (as pictured by Pietschmann 1908, p. 657, figs. 1, 2) are truncate, with concave crowns (slender, thorn-like in **lucifer,* p. 56), while those on the sides are arranged irregularly (in linear series in **lucifer*). Also, according to Pietschmann (1908, pp. 656-657) the skin of *frontimaculatus* is naked on the black areas of the lower surface and of the tail, which in **lucifer* (p. 56) are as densely denticulate as the paler sides are and the back. *E. frontimaculatus* resembles **E. pusillus* of the Atlantic in the nature of its denticles; Tanaka, in fact (1912, Pl. 22, 1912[a], p. 88) pictured and described a specimen from Misaki under that name. But it differs sharply from **pusillus* in the nakedness of the black areas on its lower surface and on its tail; in a somewhat more rearward position of its first dorsal fin relative to the pectorals, and — more conspicuously — in its color pattern, for the black belly and flank marks contrast with paler brown sides and back which is not the case in **pusillus* (compare Pietschmann 1908, Pl. 1, fig. 2 with Bigelow, Schroeder and Springer 1955, p. 3, fig. 1). *E. frontimaculatus* is so far known only from Japan.

**E. brachyurus* Smith and Radcliffe 1912 from the Philippines. This shark (Fig. 6 D, E) falls with **lucifer* in the relative position of its pectoral, dorsal and pelvic fins; in the thorn-like nature of its dermal denticles (these roughen the lower surface of its body as well as the upper); and in the arrangement in longitudinal bands of those on the upper surface, on the caudal peduncle, and on the bases of the fins. It falls further with **lucifer* in its general color pattern, with sharply outlined black flank markings, which are not shown on Smith and Radcliffe's original illustration of it. But it differs from **lucifer* in a relatively much shorter caudal fin, the upper margin of which is only about 66 per cent as long as from the tip of the snout to

the origin of the pectorals, as we can verify from recent examination of the type specimen in the U. S. National Museum (about as long as from snout to pectorals in **lucifer*). And there are five cusps on its upper teeth (three in **lucifer*), with the laterals longer, relative to the median member, than in **lucifer*. **E. brachyurus* was originally described from an adult male, 227 mm. long, taken off Jolo Island in the Philippines by "Albatross" in 1909, from 481 meters (263 fathoms). But its range extends to southern Australia, provided our union with it of *molleri* Whitley 1939 be correct (see below).

E. molleri (Whitley) 1939, from Australia. This shark described by Whitley as *Acanthidium molleri,* seems not to differ from *E. brachyurus* in any significant respect, to judge from Whitley's description or illustration (Whitley 1939, p. 265, fig. 1; 1940, pp. 147-148, fig. 163).

E. baxteri Garrick 1957, from New Zealand. This newly described *Etmopterus,* known from a female 742 mm. long, caught at 914 meters (500 fathoms) seven miles south of Kaikoura, N. Z., finds a close counterpart in *E. princeps* of the North Atlantic. But it differs so sharply from *princeps* in the respects summarized in the accompanying key (p. 63, alternatives 14-15), that the two clearly represent distinct species.

E. abernathyi Garrick 1957, from New Zealand. This well defined species, described from an immature male 338 mm. long and from a female 278 mm. long, caught at 183-366 meters off Kaikoura, N. Z., falls in the subdivision of the genus that is characterized by slender thorn-like denticles, with those on the upper part of the sides arranged in unilinear, longitudinal rows, and by a conspicuous pattern of black markings. Among the other members of this division it comes the closest to *brachyurus.* But it is separated from the latter by a much longer caudal fin and by a more forward position of the first dorsal fin, to mention only the most conspicuous differences (see Key, pp. 61, 62, alternatives 7-10). For comparison with other members of its genus, we refer the reader to Garrick's detailed account of *abernathyi* and to his excellent illustrations of it.

The U. S. National Museum also contains a female *Etmopterus,* about 270 mm. long (U.S.N.M. No. 91576) collected among the Galapagos by the "Albatross" in 1888, from 717 meters (392 fathoms), which agrees very closely with the West African

**polli*, except that such of its upper teeth as are still intact have only three cusps, contrasting with five cusps in **polli*. Unfortunately the specimen is now in such poor condition that we dare do no more than call attention to the presence in Galapagan waters of a species of *Etmopterus*, as yet undescribed.

Finally, we face the case of *E. paessleri* Lönnberg (1907, p. 5, fig. 2) from the Straits of Magellan. Lönnberg's reference of this shark to *Etmopterus* has been accepted both by Regan (1908, p. 43) and by Garman (1913, p. 229). And while Lönnberg states that lateral cusps were not visible ("nicht sichtbar") on its upper teeth, the type (and only known) specimen was so small (about 160 mm. long) that these structures may have been overlooked. Until this point can be settled its generic status must remain open. Meantime, we are content to let this species rest provisionally in *Etmopterus*. Whatever the final outcome in this regard, *paessleri* is set apart from all other members of *Etmopterus* by the nature of its dermal denticles, which are described (they have not been pictured) as having a large central spine, surrounded by several smaller spines ("einen grosseren Stachel und mehere kleinere Nebenstacheln," Lönnberg 1907, p. 5). Also, its second dorsal fin-spine is described as a little smaller than the first, just the reverse of the usual relationship.

Key to species of *Etmopterus*

1. Dermal denticles with larger central spine surrounded by several smaller spines; second dorsal fin spine smaller than first dorsal spine; lateral cusps not easily visible on upper teeth of small specimens ..... *paessleri* Lönnberg 1907. Straits of Magellan. p. 60

   Dermal denticles either truncate or with a central spine only, the latter bristle-like or thorn-like; second dorsal fin spine longer than first dorsal spine; lateral cusps on upper teeth clearly visible, even on very small specimens 2

2. Upper margin of caudal fin nearly as long as from tip of snout to rear edge of pectorals when these are laid back ..... **schultzi* Bigelow, Schroeder and Springer 1953. Northern part of Gulf of Mexico. p. 50

   Upper margin of caudal fin very little (if any) longer than from tip of snout to origin of pectorals and considerably shorter in most 3

3. Dermal denticles on sides of body truncate, without central spine 4

   Dermal denticles on sides of body with a central spine, either conical,

thorn-like, or bristle-like. 6

4. Back and upper part of sides dark brown, contrasting sharply with a black marking on either flank, and with lower surface of head and body; the black areas partially naked. .....*frontimaculatus* Pietschmann 1907. Japan. p. 58

Back and upper part of sides black or sooty like lower surface; no conspicuous flank-markings; lower surface, like upper, rough with denticles. 5

5. Denticles on sides of tail not arranged in regular longitudinal rows, and of same shape as those on sides of body; interspace between first and second dorsal fins about as long as from tip of snout to axil of pectorals .....**pusillus* Lowe 1839. p. 49 Eastern Atlantic from equatorial West Africa to the coast of Portugal, including the Cape Verde Islands, the Canaries, Azores and Madeira; also Gulf of Mexico. p. 49.

Dermal denticles on tail arranged in longitudinal rows, and more spine-like than those on the body; interspace between first and second dorsal fins shorter than from snout to first gill openings ..... *granulosus* Günther 1880. Coast of Chile, also reported from Natal coast of southern Africa and from Argentina. p. 55.

6. Denticles on sides in definite uniserial longitudinal rows 7

Denticles on sides in random arrangement, not in longitudinal rows ..11

7. Upper side of caudal fin at least not longer than from tip of snout to second gill openings. 8

Upper side of caudal fin about as long as from tip of snout to origin of pectorals. 9

8. Distance from tip of snout to first dorsal spine is about as long as from base of first dorsal spine to origin of upper side of caudal; interspace between first and second dorsal fins is only about as long as from tip of snout to level of spiracles. .....**villosus* Gilbert 1905. Hawaiian Islands. p. 57.

Distance from tip of snout to first dorsal spine is little longer than from first dorsal spine to rear end of base of second dorsal fin; interspace between first and second dorsal fins is at least as long as from tip of snout to second gill openings. ..... **brachyurus* Smith and Radcliffe 1912. Philippines; apparently including *E. molleri* (Whitley) 1939, southern Australia. p. 58.

9. Interspace between first and second dorsal fins is much shorter than from snout to first gill openings; black flank markings not conspicuous ..... **bullisi*, new species, off northeast coast of Florida. p. 50

Interspace between first and second dorsal fins is as long as from tip of snout to origin of pectorals, or longer; black flank markings conspicuous. 10

10. Distance from base of pelvics to origin of lower side of caudal is only about as long as from tip of snout to first gill openings .....
**abernathyi* Garrick 1957. New Zealand, p. 5

Distance from base of pelvics to origin of lower side of caudal is as long as from tip of snout to origin of pectorals .....**lucifer* Jordan and Snyder 1902. Japan; Atlantic off southern Africa; also reported by name from Argentina, the Philippines and the East Indies. p. 56.
For list of Philippine, East Indian, and South African records, see Herre 1953, p. 30.

11. Distance from rear end of base of pelvics to origin of lower side of caudal is at least as long as from axils of pectorals to origin of pelvics. 12

Distance from rear end of base of pelvics to origin of lower side of caudal is only about ½ as long as from axil of pectorals to origin of pelvics. 14

12. Distance from origin of pectorals to origin of pelvics is not longer than from tip of snout to origin of pectorals. .....**polli* Bigelow, Schroeder and Springer 1953. tropical West Africa. p. 50

Distance from origin of pectorals to origin of pelvics is longer than from tip of snout to origin of pectorals. 13

13. Denticles on sides below first dorsal fin are slender, bristle-like (Bigelow, Schroeder 1948, Fig. 92B); skin on lower surface of snout and in region of gill openings is rough with denticles; snout in front of spiracles about as long as from spiracles to level of axil of pectorals; black flank markings as in Figure 5H. .....
**hillianus* (Poey) 1861. Cuban and West Indian region, and northward along the American slope to the offing of Chesapeake Bay. p. 50.

Denticles on sides below first dorsal fin low, conical (Bigelow, Schroeder and Springer 1953, Fig. 10, D, E); skin on lower surface of snout

and in region of gill openings naked; snout in front of spiracles only about as long as from spiracles to level of origin of pectorals; black flank markings as in figure 5G. .....**virens*
Bigelow, Schroeder and Springer 1953. Northern part of Gulf of Mexico. p. 50

14. Interspace between first and second dorsal fins is longer than from tip of snout to axil of pectorals; distance from rear end of second dorsal to origin of upper side of caudal is only about 35 per cent as long as interspace between first and second dorsals. .....
baxteri Garrick 1957. New Zealand. p. 59

Interspace between first and second dorsal fins is only about as long as from tip of snout to origin of pectorals; distance from rear end of second dorsal to origin of upper side of caudal is about 50 per cent as long as interspace between first and second dorsals. 15

15. Dermal denticles on sides slender, bristle-like, and closely spaced (Fig. 3E); breadth of head about as great as length of snout to mouth; longest gill openings only 14-33 per cent as long as eye; black flank marks conspicuous, of shape shown in Figure 5F....**spinax* (Linnaeus) 1758. Eastern Atlantic, including Mediterranean, from the Cape Verde Islands, Morocco and the Azores to Norway, p. 49; also reported from southern Africa. p. 56.

Dermal denticles on sides low, conical to thorn-like (more slender on juveniles), and more loosely spaced (Fig. 3, F, G); breadth of head 1.2-1.4 times as great as length of snout (to mouth); longest gill openings 33-50 per cent as long as eye; flank markings not conspicuous, if visible at all. .....**princeps* Collett 1904. Faroes-Hebrides region and offing of Gibraltar in eastern Atlantic; offing of southern Nova Scotia to offing of southern New England in western. p. 50.

Genus CENTROPHORUS Müller and Henle 1837

Centrophorus Müller and Henle 1837, p. 398; 1937A, p. 115; 1841, p. 89; type species **C. granulosus* Müller and Henle, Mediterranean, considered by them and by subsequent authors in general as the same as *Squalus granulosus* Bloch and Schneider 1801, no locality given.

Generic Synonyms:

Squalus in part, Bonnaterre, 1788, p. 12, for **S. squamosus* Bonnaterre,

type locality not known; Bloch and Schneider 1801, p. 135 for **S. granulosus* Bloch and Schneider, no stated locality.

Acanthorhinus in part, Blainville 1816, p. 121, for **A. squamosus* Blainville, equals *Squalus squamosus* Bonnaterre 1788, and *A. granulosus* Blainville, equals **Squalus granulosus* Bloch and Schneider 1801.

Centrina in part, Cuvier 1817, p. 130, for *C. squamosus* Cuvier, equals **Squalus squamosus* Bonnaterre 1788.

Lepidorhinus Bonaparte 1838, type and only included species, **Squalus squamosus* Bonnaterre 1788.

Acanthias in part, Müller and Henle 1841, p. 85, for *A. uyatus* Müller and Henle, equals **Squalus uyato* Rafinesque 1810, Mediterranean.

Spinax in part, Bonaparte 1841, Pl. 57, for *Spinax uyatus* Bonaparte, equals **Squalus uyato* Rafinesque 1810.

Machephilus Johnson 1867, p. 713, type and only included species *M. dumerili* Johnson, Madeira.

Entoxychirus Gill 1862, p. 498, type and only included species *E. uyatus* Gill, equals **Squalus uyato* Rafinesque 1810.

Gaboa (subgenus of *Centrophorus*) Whitley 1940, p. 145, type and only included species, **Centrophorus harrisonii* McCulloch 1915, Victoria, Australia.

Somnispinax (subgenus of *Centrophorus*) Whitley 1940, p. 146, type and only included species, *Centrophorus nilsoni* Thompson 1930, New Zealand.

Probable Generic Synonym:

Atractophorus Gilchrist 1922, p. 48, type and only included species *A. armatus* Gilchrist, off Natal, southern Africa. For discussion, see p. 82.

Not *Squalus* Linnaeus 1758, type species *S. acanthias* Linnaeus.

Not *Spinax* Cuvier 1817, p. 129, type species *Squalus acanthias* Linnaeus 1758.

Not *Acanthias* Risso 1826, p. 131, type species *A. vulgaris* Risso, Mediterranean, equals *Squalus acanthias* Linnaeus 1758.

Generic characters. Squalinae with the fin spines laterally grooved and well exposed in most (but see p. 81 under *C. nilsoni*), the second longer than the first; lower margin of caudal with subterminal notch; teeth one-cusped in both jaws, the lowers wider than the uppers, with cusp directed strongly outward all along each side of jaw, and with the bases of successive teeth overlapping outwardly; margins of upper teeth smooth; margins of lower teeth finely serrate in some species but smooth in others; the cusp of the median lower tooth either erect and symmetrical or oblique; upper teeth subtriangular, with the

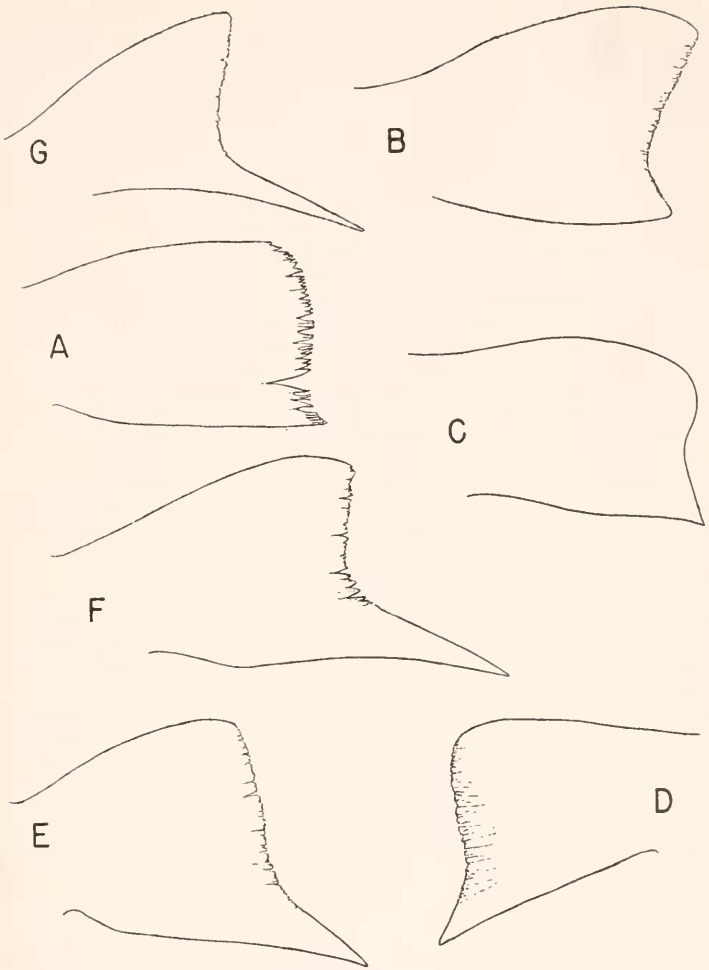

Fig. 8. Pectoral fin in different species of *Centrophorus*, adjusted to approximately equal lengths along outer margin, to show shape of inner posterior corner. A, *foliaceus*, same specimen as in Fig. 7F. B, *squamosus*, female, 1230 mm. long, southwest of Iceland. C, *steindachneri*, type specimen, after Pietschmann 1908, Pl. 1, Fig. 2B. D, *acus*, type specimen, male 820 mm. long, Japan, Mus. Comp. Zool. No. 1049. E, *uyato*, male, 429 mm. long, northern part of Gulf of Mexico, Mus. Comp. Zool. No. 38165. F, *granulosus*, female, 922 mm. long, northern part of Gulf of Mexico, U. S. Nat. Mus. No. 157833. G, *scalpratus*, Victoria, Australia, after McCulloch.

bases of successive teeth in contact along row, or slightly overlapping, the cusp erect and nearly symmetrical near center of mouth in most species, but nearly or quite as oblique as the lowers all along each side of jaw in a few species (p. 72); median upper tooth either symmetrical or oblique; inner corner of pectoral fins at least quadrate and angular, and more or less extended in most species (Fig. 8); snout to mouth in all known species, not longer than from mouth to level of origin of pectoral fins; nostrils without barbel; preoral clefts present, more or less expanded inwardly (Fig. 1B). Caudal peduncle without precaudal pits or lateral ridges; dermal denticles on sides of body low; block-like, scale-like, or conical in different species (Bigelow, Schroeder and Springer 1953, p. 270, fig. 3).

Maximum recorded lengths, 1500 mm. for **C. granulosus* and 1420 mm. for **C. squamosus* (Bocage and Capello 1866, pp. 26, 27).

Depth range. The only definite records of depths of capture that we have found are 631 meters for **foliaceus,* off Japan (Günther 1887, p. 5), and 1756 meters in Philippine waters (Smith and Radcliffe 1912, p. 679); 366-375 meters for **granulosus* (specimen in U. S. Nat. Mus. from Gulf of Mexico); 50-400 meters for **uyato* (Poll 1951, and specimens we have seen from Gulf of Mexico); "common between about 400 and 1500 meters" for **squamosus* (Grey 1956, p. 96) with one record from 1875 meters; 400 meters for *machiquensis* (Maul 1955, p. 5; and 128 to 439 meters for *scalpratus* (Whitley 1940, p. 145). While no definite information is available for any one of the group of additional species described from Japan (**acus,* **atromarginatus,* **tesselatus,* and *steindachneri*), it seems that their normal ranges are restricted to depths greater than 100-200 meters.

Remarks. The most distinctive single character of the genus (though probably not one of any great phylogenetic importance) is the angular and usually more or less extended inner corner of the pectoral fins. The range in this respect (Fig. 8) may be illustrated by **C. foliaccus* Günther 1877 of Japan, in which the pectoral inner corner is only very slightly extended or even rectangular, through conditions in **squamosus* Bonnaterre 1788, in **acus* Garman 1906 (incl. *steindachneri* Pietschmann 1907), in **uyato* Rafinesque 1810, and in *harrisonii* McCulloch 1915,

where it is extended somewhat more, and in **granulosus* Bloch and Schneider 1801, where it is still further prolonged, as it also is in *scalpratus* McCulloch 1915.

The gradation, in short, in the shape of the pectoral, is so nearly unbroken that the revival of *Lepidorhinus* Bonaparte 1838 by Garman (1913, p. 211) and of *Entoxychirus* Gill 1862 by Fowler (1941, p. 242), based on differences in this regard, serves no useful purpose, whether from the practical standpoint, or as representative of probable phylogenetic relationship. In the type specimens, in fact, of *C. nilsoni* from New Zealand (Thompson 1930, p. 277), and of **C. tesselatus* from Japan (now in the Museum of Comparative Zoology; Fig. 10 C, D), the inner corner of one of the pectoral fins is extended, but not that of the other pectoral (apparently undamaged).

Teeth. The cutting edge of the lower teeth of **C. granulosus* is described and pictured both by Müller and Henle (1841, p. 89, Pl. 33) and by Bocage and Capello (1866, p. 26, Pl. 1, fig. 3D) as finely serrate. Similarly, the reserve rows (5 in number) of our eastern Atlantic specimen of this species are finely but irregularly serrate in some places (Fig. 9A), though not in others. The lowers in the more anterior of the two rows that are visible from outside the mouth (no longer in function) also show faint traces of serration here and there. But the lowers in the functional row are slightly jagged in places, at most. And the situation is essentially similar in the case of a Gulf of Mexico specimen of **granulosus,* on which some of the lowers show microscopically fine serration, but others are merely somewhat irregular in outline, probably as the result of wear. (For further details, see Bigelow, Schroeder and Springer 1955, p. 6, Fig. 2C, p. 8). Bocage and Capello (1866, Pl. 1, Fig. 3E) picture the upper teeth of **granulosus* as finely serrate, like the lowers. But this seems to have been an error on the part of the artist, for the uppers are smooth on both of the specimens of **granulosus* that we have examined — also on all the specimens of other species of the genus that we have studied, for that matter.

In **C. squamosus,* as represented by a female about 1250 mm. long from Iceland (Fig. 10A), and by jaws of a somewhat larger individual, presumably from near the Faroes (Fig. 11B), the lowers in the outermost of the two rows that are visible from

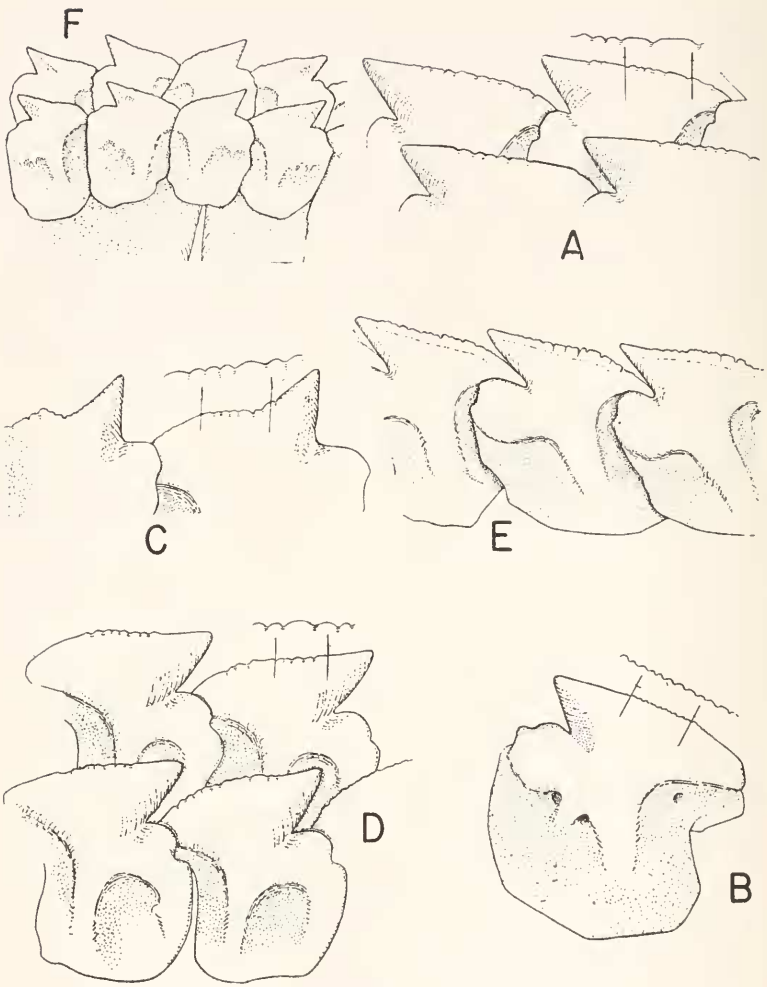

FIGURE 9

outside the mouth are finely serrate along the central part of the cutting edge, those in the reserve rows less clearly so. The lowers in the first reserve row (the edges of the functional rows are badly worn) are also unmistakably though faintly serrate in places (Fig. 9C) on the type specimen of **tesselatus*. On the type specimen of **atromarginatus* (on which the teeth are in better condition), the lowers (Fig. 9D) are irregularly but unmistakably serrate. They are described as "serrated" in *scalpratus* (McCulloch 1915, p. 98) from Australia also. And the two rows of lower teeth that are visible from outside the mouth in the type specimen of the Japanese **acus* Garman 1906 show faint and irregular traces of microscopically fine serration here and there, though not so distinctly as these appear on Garman's (1913, Pl. 12, fig. 6) illustration when the latter is viewed under a lens. In the Australian *harrisonii*, also, the edges of the lower teeth are irregularly serrate (Fig. 9E). On the other hand, we have not detected any trace of marginal serration either on the lower teeth of a juvenile male *foliaceus*, 351 mm. long, from Japan (Fig. 7G), or on those of *uyato*, whether on a 429 mm. male from the Gulf of Mexico (Bigelow, Schroeder and Springer 1953, p. 271, fig. 4) or on a 480 mm. male from the Mediterranean. Thus the presence or absence of serrations on the cutting edge of the lower teeth seems not to be a useful basis for generic separation here, though it has long been so regarded among the carcharhinid sharks.

Similarly, the degree of obliquity of the upper teeth ranges

Fig. 9. Lower teeth in different species of *Centrophorus* to show the degree of marginal serration. A, *granulosus*, male, about 855 mm. long, eastern Atlantic, Mus. Comp. Zool. No. 662, 2nd and 3rd reserve rows, x about 9. B, *squamosus*, third tooth, outermost row, from jaw of specimen taken near the Faroes, Mus. Comp. Zool. No. 39571, x about 5.5. C, *tesselatus*, male, 887 mm. long, type specimen, Mus. Comp. Zool. No. 1031, Japan, first row visible from outside the mouth, x about 15. D, *atromarginatus*, female about 870 mm. long, type specimen, Japan, Mus. Comp. Zool. No. 1455, first two rows visible from outside the mouth, x about 8. E, *harrisonii*, Australia, teeth from one of McCulloch's original specimens, made available to us through the kindness of Dr. G. P. Whitley, x about 10. F, *squamosus*, lower teeth at center of jaw of same specimen as in B, to show the obliquity of the median tooth, x about 2.4.

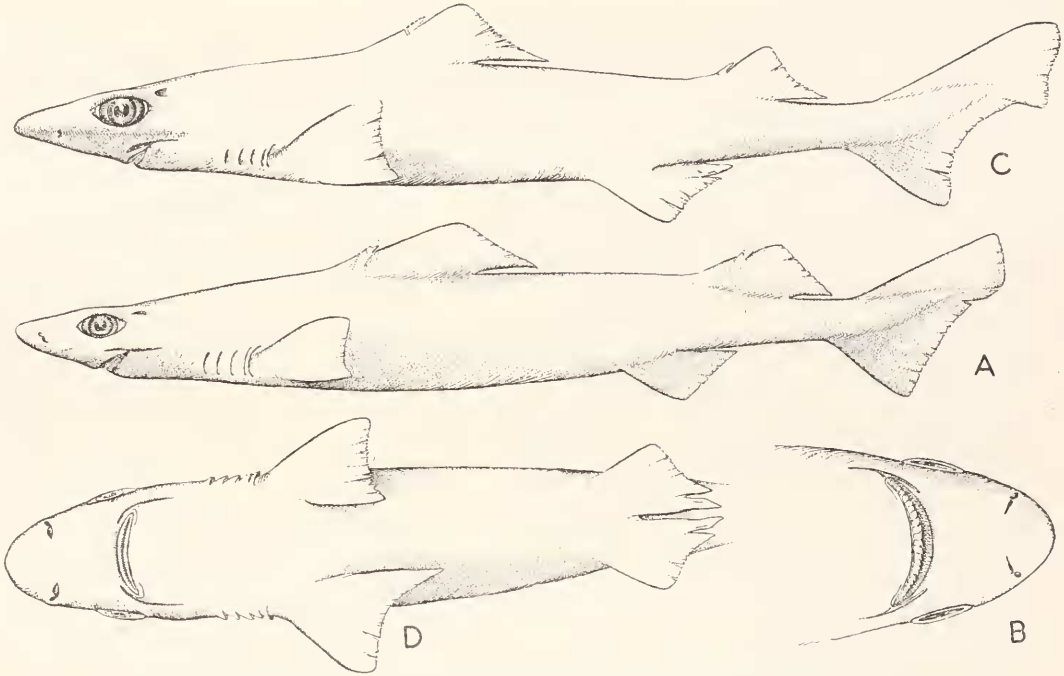

Fig. 10. A, *Centrophorus squamosus*, female, 1250 mm. long from southwest of Iceland. B, ventral view of head of same. C, *Centrophorus tesselatus*, male, 887 mm. long, type specimen, Mus. Comp. Zool. No. 1031, Japan. D, ventral view of anterior part of trunk of same, to show the difference in shape between the two pectoral fins of this particular specimen.

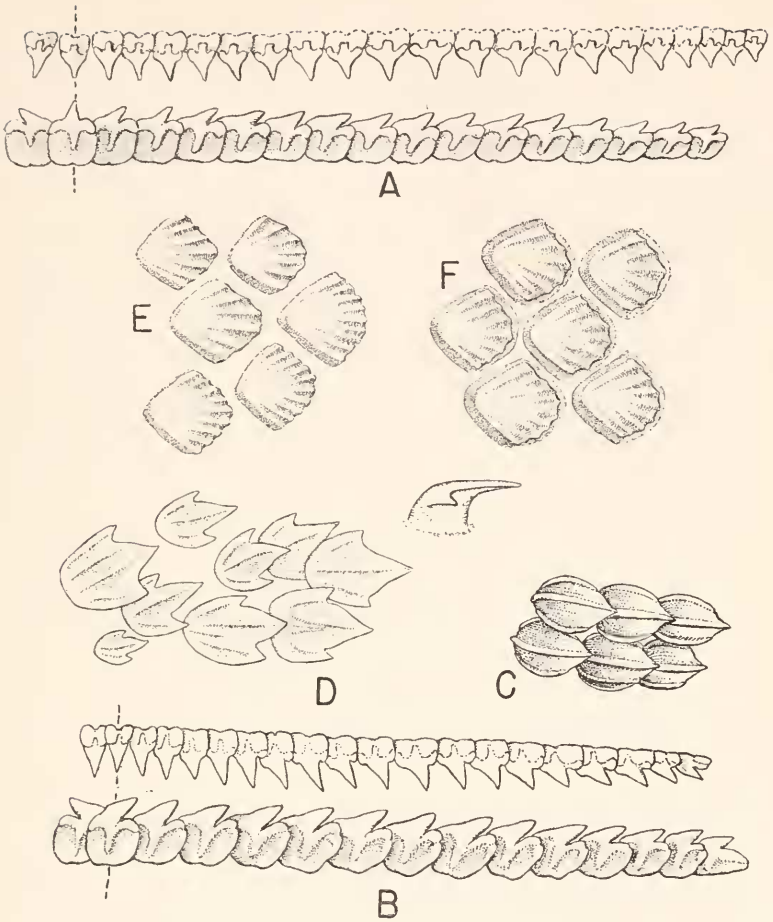

Fig. 11. A, *Centrophorus tesselatus,* same specimen as in Fig. 9C, upper and lower teeth, left hand side of mouth, x about 3. B, *Centrophorus squamosus,* female, about 1100 mm. long, from southwest of the Faroes, upper and lower teeth, left hand side of mouth, x about 1.3. C, *Centrophorus squamosus,* same specimen as in B, denticles from side below first dorsal fin, x about 5.5. D, *Centrophorus acus,* male, 810 mm. long, type specimen, Mus. Comp. Zool. No. 1049, Japan, denticles from side below first dorsal fin, x about 15. E, *Centrophorus atromarginatus,* female, about 850 mm. long, type specimen, Mus. Comp. Zool. No. 1455, denticles from side below first dorsal fin, x about 17. F, *Centrophorus tesselatus,* same specimen as in A, denticles from side, x about 17.

from the state in **granulosus* and in **atromarginatus* (Garman 1913, Pl. 13, fig. 2), where those along the central sector of the jaw are erect and symmetrical, or nearly so, to the state in **uyato* (Bigelow, Schroeder and Springer 1953, p. 271, fig. 4) and in *harrisonii* (McCulloch 1915, p. 99, Pl. 14, fig. 3), where this is true only of the first few teeth next to the midpoint of the jaw, the teeth farther out along the latter being nearly or quite as strongly oblique as the lower teeth are.

As remarked above (p. 21), the specimen on which Johnson (1867) based his new genus and species *Machephilus dumerili*, but which Vaillant (1888, p. 70), Garman (1913, p. 212), Rey (1928, p. 440), and Bigelow, Schroeder and Springer (1953, p. 224) have considered as identical with **Centrophorus squamosus* (Bonnaterre) 1788, had a symmetrical tooth at the center of the lower jaw. Accordingly Vaillant (1888, p. 70), followed by Rey (1928, p. 443), included the presence or absence of a symmetrical median lower tooth as alternative between two varieties of **squamosus*. Conditions in this respect among specimens of *Centrophorus* that we have examined are as follows: **granulosus* (male about 855 mm. long, Europe, and female 922 mm., Gulf of Mexico); **squamosus* (2 females about 1250 and 1280 mm. long from Iceland and jaws of 4 somewhat larger specimens, probably from west of the Faroes, Fig. 11B); **acus* (type specimen, male about 820 mm., Japan); **atromarginatus* (type specimen, 857 mm., Japan); and **foliaceus* (male, 351 mm. long, Japan), the cusp of the median lower tooth is about as oblique as the cusps of the successive teeth outward, in each of the rows that are visible from outside the mouth. On the other hand, the cusp of the median lower tooth is erect and symmetrical in both these rows on the type specimen of **C. tesselatus* from Japan (Fig. 11A). And the two specimens we have seen of **C. uyato* are intermediate between these two extremes, the cusp of the median lower tooth being strongly oblique on a male of 480 mm. from Nice, France, but only very weakly so, as well as smaller than that of the succeeding teeth on another male of 445 mm. from the Gulf of Mexico (Bigelow, Schroeder and Springer 1953, p. 271, fig. 4). Evidently the degree of obliquity of the cusp of the median lower tooth is not an appropriate basis for generic separation here.

Dermal denticles. In some members of the genus the denticles

on the sides of the trunk are scale-like and overlapping, the rear edges even or tridentate, and with the ridges on the outer surface either parallel or diverging slightly rearward. In other species the denticles are more block-like or conical-thorn-like, not overlapping, more or less pointed, with the ridges converging rearward. And Rey's (1928, p. 239, fig. 143) account of the denticles of **C. granulosus* as more pointed on juvenile specimens than on adults seems actually to have been based on a specimen of **C. uyato* (Rey 1928, Pl. 3, fig. 2), a species for which pointed denticles are diagnostic. The shape of the denticles, indeed, is the most obvious character among those likely to serve as alternative in this genus as between groups of species. But to subdivide *Centrophorus* generically on this basis, or by the other minor characters on which Whitley (1940, pp. 145, 146) based his subgenera *Gaboa* (type *Centrophorus harrisonii* McCulloch 1915) and *Somnispinax* (type *Centrophorus nilsoni* Thompson 1930), seems not to serve any useful purpose, the total number of species concerned being so small, and their resemblance, in general, being so close one to another.

Nomenclatural status of the type species. The original description by Bloch and Schneider (1801, p. 135) of their *Squalus granulosus* reads as follows: "Sq. bruneus cute granulosa, aculeis 2 robustis compressis, postice parum incu ruis, intus concavis, primo in initio pinnae dorsi, secundo in initio mesurae, pinnis brevibus, dorsali pectoralibus propinquiorae quam ventralibus remotissimis, mesura caudale vicina, foraminibus temporum remotis, lunatis."

Obviously this is not enough to place Bloch and Schneider's five-foot specimen, whether as to genus among the Squalinae, or as to species, for it does not mention either the shape of the pectoral fins or the nature of the teeth. It is therefore fortunate for the sake of nomenclatural stability that while Müller and Henle's (1841, p. 89, Pl. 33) description and illustrations of their **granulosus* were based on an alcoholic specimen from near Sicily, they did have, for comparison, a dried specimen in Berlin from Bloch's collection, probably the one on which Bloch and Schneider's 1801 account was based, for they mention only the one. Müller and Henle's identification of their "*granulosus*" with the "*granulosus*" of Bloch and Schneider 1801 is therefore to be accepted — unless re-examination of the

type specimen (if still in existence) should eventually prove otherwise. This, in turn, implies that Müller and Henle's very excellent description and illustrations take precedence over the several accounts by subsequent authors, as the underlying basis for the comparison of species within the genus *Centrophorus*.

Species. The following named species, listed in chronological order, fall in *Centrophorus* as defined above (p. 64): **Squalus squamosus* Bonnaterre 1788 eastern North Atlantic (Figs. 1B; 8B; 9B; 10A, B; 11B, C), including *Machephilus dumerili* Johnson 1867; **S. granulosus* Bloch and Schneider 1801 including *Centrophorus braganzae* Regan 1906), type species, eastern North Atlantic (including the Mediterranean) and Gulf of Mexico; **Squalus uyato* Rafinesque 1810, eastern Atlantic (including the Mediterranean) and Gulf of Mexico (Fig. 8E); *Centrophorus moluccensis* Bleeker 1860, Amboina; *Centrophorus lusitanicus* Bocage and Capello 1864, coast of Portugal; **Centrophorus foliaceus* Günther 1877, Japan (Fig. 7F-I); **C. acus* Garman 1906, Japan (Fig. 11D); **C. tesselatus* Garman 1906, Japan (Figs. 9C, 10C, 11A); *C. steindachneri* Pietschmann 1907, Japan (Fig. 8C); **C. atromarginatus* Garman 1913, Japan (Figs. 9D, 11E); *C. harrisonii* McCulloch 1915, Australia (Fig. 9E); *C. scalpratus* McCulloch 1915, Australia (Fig. 8G); *C. nilsoni* Thompson 1930, New Zealand; and *C. machiquensis* Maul 1955, Madeira.

The specimen from southeastern Africa, described by Gilchrist (1922, p. 48) as *Atractophorus armatus,* is also provisionally referred here to *Centrophorus* (for discussion, see p. 82).

The members of the genus may be segregated by the shape of the denticles on the sides of the body, in three groups: A, denticles block-like, close set but not overlapping; B, denticles scale-like and overlapping more or less; C, denticles spur-like or conical-thorn-like and more widely spaced.

In the Atlantic, group A is represented by **C. granulosus,* by *lusitanicus* if this finally proves a distinct species (see below), and by the newly described *C. machiquensis,* which may prove to be identical with **granulosus* when a larger number of specimens of it have been examined; group B is represented by **squamosus;* group C by **uyato.* The distinctive features of **granulosus,* **squamosus* and **uyato* — all of which are fairly

well known now — are discussed elsewhere (Bigelow, Schroeder and Springer 1953, pp. 224-225; 1955, p. 7).

The status of *lusitanicus* remains uncertain. Originally described as distinct from **granulosus* by Bocage and Capello in 1864 but definitely classed by them in 1866 with **granulosus, lusitanicus* was revived as a separate species by Günther (1870, pp. 420-421), and was so regarded both by Regan (1908) and by Garman (1913, p. 199). Again relegated to the synonymy of **granulosus* by Rey (1928, p. 436), it has been revived by Nobre (1935, p. 449). And Mr. G. E. Maul informs us that the first dorsal fin of a specimen which he has examined in the British Museum is larger than in **granulosus*, as appears from the following tabulation.

Proportional dimensions, in per cent of total length, of (A) *Centrophorus lusitanicus*, male, 742 mm. long, coast of Portugal, based on data furnished to us by Mr. G. E. Maul from a specimen in the British Museum, and (B) **Centrophorus granulosus*, female, 922 mm. long, Gulf of Mexico (U. S. Nat. Mus., No. 157833).

	A	B
Snout length in front of mouth	9.4	9.1
First dorsal fin: vertical height	7.4	5.4
Base, from anterior origin of spine	11.7	8.5
Free rear margin of fin	7.3	6.9
Second dorsal fin: vertical height	6.1	5.0
Base, from anterior origin of spine	6.6	5.7
Free rear margin of fin	4.0	4.5
Caudal fin: length of upper margin	19.7	20.3
Distance from snout to: origin of first dorsal spine	32.1	34.8
origin of second dorsal spine	67.0	69.2
upper origin of caudal fin	80.3	79.7
origin of pectoral fins	22.2	22.2
origin of pelvic fins	60.7	58.7
Interspace between: origin of first dorsal spine and second dorsal spine	34.9	34.4
base of second dorsal and lower origin of caudal	6.6	6.0
Distance from: origin of pectorals to origin of pelvics	38.4	37.6
origin of pelvics to lower origin of caudal	15.8	18.1

Until a larger number of specimens have been measured to determine how wide the range of variation may be, it must

remain an open question whether *lusitanicus* deserves recognition as a species separate from *granulosus*.

The situation is not clear for the species of *Centrophorus* that are known from the northern Pacific (all of them from Japan). Among these, group A (with block-like denticles closely spaced in quincunx arrangement) is represented by **tesselatus* and by **atromarginatus*. The demarcation between these two seems clear cut, from our examination of the type specimens in the Museum of Comparative Zoology. Thus the interspace between the rear end of the base of the first dorsal fin and the point of emergence from the skin of the second dorsal spine is as long as from tip of snout to axils of pectorals in **atromarginatus*, but is only as long as from the snout to origin of pectorals in **tesselatus*. Also, the inner corner of the pectoral fins is extended somewhat farther, the second dorsal spine is noticeably longer, and the cusps of the lower teeth are not only more strongly oblique but their cutting edge less deeply concave in **atromarginatus* than in **tesselatus*. Furthermore, the cusp of the median lower tooth, which is strongly oblique on the type specimen of **atromarginatus*, is erect and symmetrical on the type specimen of **tesselatus*, as noted above (p. 72). But this last difference may be a sexual one.

It remains an open question whether **atromarginatus* is separable from **granulosus* of the Atlantic. At least, our comparison of the type specimen of the former (a female of 850 mm.) with a male **granulosus* of 860 mm. from the eastern Atlantic, with a female of that species, 922 mm. long from the Gulf of Mexico (Bigelow, Schroeder and Springer 1955, fig. 2), and with Müller and Henle's (1841, Pl. 33) excellent picture of a **granulosus* from the Mediterranean, has not revealed any differences that might seem of specific rank, unless it be that the gill openings are not as long in the Japanese form (third gill is about 64 per cent as long as distance between nostrils) as in our Gulf of Mexico specimen (third gill about 80 per cent as long as distance between nostrils). And while Garman (1913, p. 197) described the teeth of **atromarginatus* as "not serrate," the lowers of the type specimen do show traces of fine serrations along the cutting edge (Fig. 9D) much as in the case of **granulosus* (Fig. 9A), in **tesselatus* also, for that matter (Fig. 9C). Pietschmann (1908, p. 663), in fact, has reported under

the name *granulosus* two Japanese specimens of *Centrophorus,* respectively 536 mm. and 908 mm. long, that he had compared with two *granulosus* of corresponding sizes from the Mediterranean. But the actual identity of his Japanese specimens calls for verification (if they are still in existence) for their denticles are described (Pietschmann 1908, pp. 663-667) as differing in shape from those of **granulosus* of the Atlantic. Pietschmann also united both **tesselatus* and **acus* Garman with **granulosus.* But as implied in the foregoing discussion, **tesselatus* differs from **atromarginatus.* And the denticles on the sides of the body of **acus* (no figures of which had appeared when Pietschmann wrote) differ widely from those of **granulosus,* for they are scale-like, with tridentate rear margins (Fig. 11D).

The **granulosus-*tesselatus-*atromarginatus* group of the Northern Hemisphere has a close ally in the Southern Hemisphere of the Pacific in *scalpratus* of Australian waters, except that McCulloch's (1915, Pl. 13, figs. 2-7) illustrations show the denticles on its sides as more pointed than those of **granulosus* of the Atlantic and Gulf of Mexico (Bigelow, Schroeder and Springer 1953, p. 270, fig. 3A; 1955, fig. 2D), or of the Japanese representative of the latter (p. 76). Other differences suggested by McCulloch's illustrations of *scalpratus* may be due to different methods of measurement, etc. The embryo from Amboina that was described by Bleeker in 1860 as *C. moluccensis* appears also to fall in this same group, for Regan (1908, p. 51), who saw the type specimen, located it in the subsection of the genus with "posterior angle of pectoral fin considerably produced and acutely pointed." And the little else that is known of its fins and bodily dimensions is consistent with this. But the shape of its denticles is not known.

Group B, with scale-like denticles (p. 74), is represented in the northwestern Pacific by **foliaceus,* originally described from Japan, and reported by name (with very brief comment) from deep water (960 fathoms) among the Philippines (Smith and Radcliffe 1912, p. 679); by **acus* from Japan; and by *steindachneri,* also from Japan. Among these, *steindachneri,* with tridentate flank denticles and with the inner corner of the pectorals only slightly extended (Fig. 8C; Pietschmann 1908, p. 676, text fig. 3; Pl. 1, fig. 1) agrees so closely with the type specimen of **C. acus* as to make it reasonably certain that the two represent

but a single species, to be named *acus* on the ground of priority. **Acus,* in turn, is allied to **foliaceus.* But it differs from the latter in the evident extension of the inner corner of its pectoral fins, for these are not appreciably extended in **foliaceus,* either as they are represented by Günther (1887, p. 5, Pl. 2, fig. A), or as they appear on two immature males of **foliaceus,* respectively 325 and 350 mm. long, from Japan (U. S. Nat. Mus., Nos. 161517 and 161518) that we have examined (Fig. 7F). The dermal denticles, also, on the sides of the type specimen of **acus* differ conspicuously from those of **foliaceus,* for while they are tridentate in both cases, they are not only broader, relatively, with shorter marginal teeth and less regularly overlapping in **acus* (Fig. 11D) than in **foliaceus* (Fig. 7H), but so much smaller relatively that the one species is separable from the other at a glance by this character alone. **C. foliaceus,* indeed, is by far the roughest-skinned species of *Centrophorus* that we have seen. **Acus* is also firmer-bodied than **foliaceus,* at least in the preserved state, and it is of a paler hue below than above, whereas the specimens of **foliaceus* we have seen are of as dark a chocolate brown below as above. The species **acus* may, therefore, be retained as distinct, at least until someone re-examines the type specimen of **foliaceus,* now in the British Museum. (For an account of **acus,* with beautiful illustrations, see Garman 1913, p. 199, Pl. 12, figs. 5-8.)

The accounts of **foliaceus* by Günther (1887, p. 5) and by Jordan and Fowler (1903, p. 631), do not especially emphasize the characters now known to be diagnostic of species within the genus *Centrophorus.* A more detailed account from this point of view, with measurements, is therefore included here (p. 78).

Centrophorus foliaceus Günther 1877

Figure 7F-I

Study material. Immature male, 351 mm. long, U. S. Nat. Mus. No. 161518, Okinosa, Japan.

Proportional dimensions of specimen listed above, in per cent of total length.

Snout, length in front of: outer ends of nostrils 3.4; mouth 10.8.
Eye: length, 4.8.
Mouth: breadth, 7.6.

Nostrils: distance between inner ends, 4.0.

Gill opening lengths: First, 2.1; second, 2.4; third, 2.4; fourth, 2.4; fifth 2.0.

First dorsal fin: vertical height, 5.0; length from imbedded base of spine to rear end of base of fin, 9.0.

Second dorsal fin: vertical height, 5.0; length from imbedded base of spine to rear end of base of fin, 8.0.

Caudal fin: upper margin, 21.1; lower anterior margin, 15.7.

Pectoral fin: outer margin, 10.8; inner margin, 7.7; width, 7.3.

Distance from snout to: imbedded base of first dorsal spine, 36.2; imbedded base of second dorsal spine, 65.5; upper origin of caudal, 78.9; origin of pectorals, 25.4.

Interspace between: rear end of base of first dorsal and imbedded base of second dorsal spine, 22.5; rear end of base of second dorsal and upper origin of caudal, 5.7; base of pelvics and lower origin of caudal, 12.4.

Distance from origin to origin of: pectorals and pelvics, 33.7; pelvics and caudal, 17.6.

Teeth: $\frac{16\text{-}1\text{-}16}{14\text{-}14}$

Head, to origin of pectorals, about ⅓ of trunk to upper origin of caudal fin; snout in front of mouth about 42 per cent of head to pectorals; eye about 19 per cent as long as head; distance from tip of snout to front of eye about 29 per cent of head; distance between inner ends of nostrils about 37 per cent as long as snout to mouth; longest gill openings (2nd, 3rd and 4th) about half as long as eye; mouth transverse, scarcely arched; distance between inner ends of preoral clefts about 1.75 times as great as between nostrils.

Upper teeth short, triangular, the median tooth erect, symmetrical, but the subsequent teeth increasingly oblique outward along the jaw, with the inner edges of those toward the corners of the mouth nearly horizontal; the lowers wider than the uppers, the cusps directed so sharply outward as to form a nearly unbroken cutting edge paralleling either side of the jaw. Cutting edge of lowers perfectly smooth, both in the reserve rows and in the outermost of the two rows visible from outside the mouth; the 2nd row slightly irregular, but not definitely serrate. The condition of the specimen does not allow us to determine whether or not there was a symmetrical median tooth in the lower jaw.

Dermal denticles scale-like, close set and largely overlapping, those on upper and lower sides of snout ovate, but those on body as a whole tridentate, lanceolate in general form, with the median tooth much the longest, on short pedicle, rising steeply from the skin and with high median crest; those on back, anterior to first dorsal spine, the largest. Length of first dorsal fin, measured from anterior side of imbedded origin of spine about 2.5 times as long as distance between nostrils; interspace between rear end of base of first dorsal fin and anterior edge of imbedded base of second dorsal spine about as long as from tip of snout to second gill openings. Second dorsal fin similar in shape to first dorsal, about 90 per cent as long, basally, as first, similarly measured (see above). Dorsal spines both well exposed; exposed portion of second about 1.5 times as long as that of first; distance between first and second spines, at points of emergence from the skin, about 1.5 times as long as from tip of snout to first gill openings. Interspace between rear end of base of second dorsal fin and origin of upper side of caudal about as long as from point of emergence from skin of second dorsal spine to rear end of base of second dorsal fin. Caudal fin about 20 per cent of total length, of the shape shown in Figure 7F. Distance from origin of lower side of caudal to rear end of bases of pelvics about as long as from rear edge of eye to origin of pectoral fins. Rear tips of pelvics (when laid back) about in a line with point of emergence from skin of second dorsal spine; origin of pelvics anterior to imbedded base of second dorsal spine by a distance about as long as from rear end of eye to first gill openings. Pectorals with outer margin about as long as from eye to fourth gill openings; outer corner broadly rounded; distal margin weakly sinuous, reaching, when laid back, about even with imbedded base of first dorsal spine; inner corner angular, with a few of the horny rays slightly extended (Fig. 8A).

Color. Plain dark brownish gray above and below; the rear margins of pectorals and tip of dorsals pale edged, after many years in alcohol.

Remarks. **C. foliaceus* is recognizable at a glance, so widely does its dermal armature, with close-set, strongly tridentate, high-crested denticles, rising steeply from the skin, differ from that of every other *Centrophorus* that we have seen, or that has

been pictured. Other distinctive characters for it (within the genus *Centrophorus*) are: the shape of the inner corner of its pectoral fins (p. 66), the lack of any abrupt transition from the general contour of its back to the rising slope of the first dorsal fin, and the pronounced obliquity of its teeth, uppers as well as lowers, as described above (p. 79).

In all these respects the specimen here described agrees with Günther's (1887, p. 5, Pl. 2, fig. A) account of a 470 mm. (18½ inch) male, except that its inner pectoral corner is very slightly extended ("rectangular, not produced" according to Günther), and that it is only the median upper tooth that is erect in the upper jaw, the lateral upper teeth being strongly oblique (see above), whereas Günther characterized "the anterior teeth of the upper jaw" as erect, the laterals as "slightly oblique." These slight differences do not seem to call for recognition in nomenclature on the basis of so few specimens.

The Japanese **foliaceus* resembles **squamosus* of the eastern North Atlantic in its bodily proportions in general, in the relative locations of its fins, and in the scale-like nature of the denticles on the sides of its trunk. But it differs from **squamosus* in the quadrate outline of the inner corner of its pectoral fins (definitely though only slightly extended in **squamosus* cf. Fig. 8A with Fig. 8B), and in the narrower, more regularly tridentate and more steeply elevated denticles (cf. Fig. 7H with Fig. 11C), so that the two species clearly are separable, the one from the other.

The Northern Hemisphere species with scale-like denticles are represented in the Southern Hemisphere by *nilsoni* of New Zealand (Thompson 1930, p. 277, Pl. 44). *Nilsoni* falls close to **acus* in the shapes of the inner corner of its pectoral fins and of the denticles on the sides of its trunk. But its fin-spines are described by Thompson (1930, p. 277) as "low and largely covered," a character which (if normal) sets it apart.

The North Atlantic **uyato,* with conical-thorn-like denticles on its sides and with the inner pectoral corner moderately extended, is similarly replaced in the South Pacific by *harrisonii* of Australian waters. Going back a step further in shark history, the embryo reported from Port Jackson, Australia, many years ago by Steindachner (1867, p. 333) under the name *Acanthias uyato* Rafinesque, may have been the first specimen

of *harrisonii* to come under scientific observation. On the other hand, Whitley (1934, p. 199) has suggested that it may have been a *Squalus*, a view supported by Steindachner's description of it as marked with large white spots on its back. However this may be, the cutting edge of the lower teeth, which are smooth in the Atlantic **uyato* (p. 69), are irregularly serrate (Fig. 9E) in *harrisonii* (described as imperfectly so by McCulloch 1915, p. 99). And other differences between the Atlantic and Indo-Pacific populations may come to light when adequate series of specimens from the two ocean areas have been compared.

Finally, we face the case of *Atractophorus armatus* from the Natal coast of southern Africa, the type specimen of which seems to have been a typical *Centrophorus* in all respects, except that the tip of its second dorsal fin spine was described and pictured as "barbed, like an arrowhead" (Gilchrist 1922, p. 48, Pl. 7, fig. 3). Unfortunately, the type specimen of *armatus* is no longer to be found.[11] But the collection of the Government Marine Survey of South Africa does contain a juvenile shark, 330 mm. long, apparently an *armatus*, the second dorsal fin spine of which (while not two-barbed) bears a single, wing-like expansion on its rear side, close to its tip (Fig. 7J). And any conformation of the spine tip, other than tapering to a point (if normal) makes *armatus* unique among known sharks, whether modern or fossil. We may either accept this feature as justifying the generic separation of *Atractophorus* from its parent genus *Centrophorus*, or we may transfer *armatus* to *Centrophorus*, as the genus in which it would fall on the basis of ancestral relationship, were it not for the single character in question. We choose this last alternative, partly because we see no useful purpose to be served in acting otherwise; partly because this choice seems the more likely of the two to focus attention on *armatus* when additional specimens come to hand; and partly because of the chance that the peculiar conformation of the second dorsal spine tip on the two specimens that have been examined may have represented an abnormality, or may have been the result of accidental damage.

If *armatus* is, in fact, a *Centrophorus*, its closest relationship is with *harrisonii*, with which — and with **uyato* of the North

[11] We are so informed by Prof. J. L. B. Smith, who has made a special search for it in the collection of the Government Marine Survey of South Africa.

Atlantic — it shares pectoral fins with extended inner corner (but shorter from origin to rear tip than from tip of snout to level of first gill openings), and denticles on sides of body that are described as acuminate, with many sharp ridges (Gilchrist 1922, p. 49).

Key to species of *Centrophorus*

1. Denticles on sides of trunk scale-like, overlapping, the ridges on their outer surface (if more than one) parallel or diverging slightly rearward 2
   Denticles on sides of trunk block-like or conical-thorn-like, not overlapping; the ridges on their outer surface converging rearward, if at all 5
2. Denticles on sides of body not definitely tridentate (Fig. 11C) ..... **squamosus* Bonnaterre 1788. Northeastern Atlantic. p. 74
   Denticles on sides of body regularly tridentate (Figs. 7H, 11D) 3
3. Inner corner of pectoral fins quadrate, not appreciably extended (Fig. 8A); dermal denticles on sides of body as in Figure 7H ..... **foliaceus* Günther 1877. Japan; also reported by name from the Philippines (Smith and Radcliffe 1912, p. 679), and from New Zealand (Richardson 1956, p. 7). p. 78
   Inner corner of pectoral fins definitely extended, though not greatly so (Fig. 8D); denticles on sides of body as in Figure 11D) 4
4. Both of the dorsal fin spines prominent and well exposed ..... *acus* Garman 1906, Japan. p. 77
   Both of the dorsal fin spines low and largely covered ..... *nilsoni* Thompson 1930, New Zealand; p. 81
5. Pectoral fin, from origin to inner rear corner, about as long as from tip of snout to level of fourth gill openings ..... *scalpratus* McCulloch 1915, Australia. p. 74
   Pectoral fin from origin to inner rear corner shorter than from tip of snout to level of first gill openings 6
6. Denticles on sides of trunk block-like, quadrate, closely spaced in quincunx arrangement; upper teeth erect and symmetrical, or nearly so, all along central part of jaw 7
   Denticles on sides of trunk conical-thorn shaped, loosely spaced in random arrangement; upper teeth strongly oblique, except for the first few next to the mid-point of the jaw, which are erect 8
7. Distance from rear end of base of first dorsal fin to point of emergence

from the skin of second dorsal spine is as long as from tip of snout to axil of pectorals; exposed part of second dorsal fin spine is about 75 per cent as long as distance between nostrils .....
granulosus Bloch and Schneider 1801 (including *lusitanicus* Bocage and Capello 1864); Mediterranean with neighboring eastern Atlantic, Gulf of Mexico, p. 73; and reported by name from tropical West Africa (Cadenat 1950, p. 101); also *machiquensis* Maul 1955, Madeira (p. 74); and *atromarginatus* Garman 1913, Japan (see discussion, pp. 76-77).

Distance from rear end of base of first dorsal fin to point of emergence from the skin of second dorsal fin spine is only about as long as from tip of snout to origin of pectorals; exposed part of second dorsal spine only about 40 per cent as long as distance between nostrils .....
tesselatus Garman 1906, Japan. p. 74

8. Cutting edges of lower teeth smooth .....*uyato* Rafinesque 1810. Mediterranean, eastern tropical Atlantic along the African coast from Senegambia (Rochebrune 1883-1885, p. 24) to Lat. about 20° S (Poll 1951, p. 65); also Gulf of Mexico. p. 74

Cutting edges of lower teeth irregularly serrate (Fig. 9E) ..*harrisonii* McCulloch 1915. Australia. p. 74

Position uncertain: *moluccensis* Bleeker 1860, Amboina; also *armatus* Gilchrist 1922, southeastern Africa (p. 82).

Genus CENTROSCYMNUS Bocage and Capello 1864

Centroscymnus Bocage and Capello 1864, p. 263; 1866, p. 29; type species **C. coelolepis* Bocage and Capello, off Portugal.

Generic Synonyms:

Centrophorus in part, Günther 1870, p. 423, for *C. coelolepis* Günther, equals **Centroscymnus coelolepis* Bocage and Capello 1864; Thompson 1930, p. 277, for *C. waitei* Thompson, New Zealand.

Centroselachus Garman 1913, p. 206, type species **Centrophorus crepidater* Bocage and Capello 1864, off Portugal.

Proscymnodon (subgenus) Fowler 1934, p. 239, type and only included species *Centrophorus plunketi* Waite 1909, New Zealand.

Scymnodon in part, Fowler 1941, p. 225, for *Centrophorus plunketi* Waite 1909, New Zealand.

Not *Scymnodon* Bigelow, Schroeder and Springer 1953, p. 230, for *Scymnodon melas* Bigelow, Schroeder and Springer 1953, p. 233, fig. 5, which is a young stage of *Centroscymnus coelolepis* (p. 100).

Generic characters. In general as in *Centrophorus* (p. 64), except with inner corner of pectoral fins broadly rounded (this is the most conspicuous difference between the two genera); the upper teeth more slender than the lowers, lancet shaped, those along central sector of mouth nearly as long as those midway out along either side of upper jaw; the successive teeth in the functional row not in contact basally, or hardly so; lower teeth smooth edged, the successive cusps directed so strongly outward as to form a nearly continuous cutting edge; median lower tooth not symmetrical; second dorsal fin spine, like first, either exposed more or less at tip, or entirely enclosed in the skin; dermal denticles on sides of body low, scale-like, with tridentate margins on young specimens in some species, and probably in all, also on adults in some species, but replaced later in growth in other species by denticles with evenly rounded margins and concave crowns; preoral clefts short in some species but so long in others as to leave only a narrow gap between their inner ends (see discussion, p. 87), considerably expanded inwardly in species where they are short (Fig. 1C) but not appreciably so in those where they are longest (Fig. 1D).

Maximum recorded length 1140 cm. for *C. coelolepis* (Bocage and Capello 1866, p. 31) and 1414 for *C. plunketi* (Waite 1910, p. 384).

Depth range. Centroscymnus coelolepis (p. 88), the shoalest record for which has been 329 meters, has its center of distribution between 400 meters and 2000 meters according to locality, and has been taken down to about 2700 meters (maximum yet recorded for any shark). It may fairly be classed as the deepest living of modern sharks. (For further details see Bigelow and Schroeder 1948, p. 498, and Grey 1956, pp. 97-98.) Depth records for the other members of this genus are 270-920 meters for *crepidater* off Iceland (Saemundsson 1922, pp. 192, 196, as *Centrophorus jonsonii*); 220 meters for *plunketi* (Waite 1910, p. 384); 780 meters for *rossi* (Alcock 1898, p. 144); and 512 meters for *fuscus* (Gilchrist and von Bonde 1924, p. 3).

Remarks. Teeth. The only characters mentioned by Bocage and Capello (1864, p. 263; 1866, pp. 19-20, 24, 29) in their successive generic diagnoses of *Centroscymnus* that contrast with their diagnosis for *Centrophorus* (1866, pp. 19, 22) were that the upper teeth of the former are awl-shaped and loosely spaced ("subuliformes écartés") and that its first dorsal fin spine is almost entirely enveloped by the skin. But a much more conspicuous difference than either of these is the rounded inner corner of the pectorals of *Centroscymnus,* as contrasted with their angular inner corner in *Centrophorus* (p. 66). Similarly, the only alternative character in their original diagnosis of *Centroscymnus,* as contrasted with *Scymnodon,* is the shape of the lower teeth, which Bocage and Capello characterized for the former as not unlike those of *Centrophorus* (i.e. as oblique, without symmetrical median tooth), but for *Scymnodon* as with symmetrical median tooth, the first tooth outward from it on either side erect, the succeeding teeth as increasingly oblique toward corners of mouth ("dens medianus impar, post eum dantes premum erecti, deinde versus angulum oris magis ac magis decumbentes," Bocage and Capello 1864, p. 263). But a second difference between the type species of *Centroscymnus* (**coelolepis* Bocage and Capello 1864) and of *Scymnodon* (**ringens* Bocage and Capello 1864), equally diagnostic and much more conspicuous, is that while the upper teeth along the central sector of the mouth are nearly as long as those midway out along each side of the jaw in *Centroscymnus,* they are much shorter than those midway along the jaw in *Scymnodon.* The value of this feature as a diagnostic character seems first to have been realized by Rey (1928, p. 486, fig. 152).

Dermal denticles. In the adults of some species (*plunketi* Waite 1910, New Zealand; **crepidater* Bocage and Capello 1864, eastern Atlantic) that are referable to *Centroscymnus* by their dentition, the denticles on the sides of the trunk are tridentate in outline, the outer surface sculptured with longitudinal ridges. In the adults of others (**coelolepis* Bocage and Capello 1864, both sides of the North Atlantic; *cryptacanthus* Regan 1906, Madeira; **owstoni* Garman 1913, Japan), they are rounded in outline, with smooth, concave crowns; also in *fuscus* Gilchrist and von Bonde 1924, southern Africa, so far as the concavity

of the crowns is concerned.[12] But it has been found by Tortonese (1952, p. 386, corroborated by Bigelow and Schroeder 1954, p. 47) that the rounded denticles of the adult **coelolepis,* and apparently those of **owstoni* as well (Bigelow and Schroeder 1954, p. 50), are preceded at early stages in growth (as proven by embryos of known parentage) by tridentate forms, the replacement of denticles of the juvenile shape by others of the adult shape taking place when a given specimen is half to two-thirds grown. For further details we refer the reader to our earlier account (Bigelow and Schroeder 1954, p. 47, fig. 2). It follows from this that our earlier acceptance of the shape of the denticles (Bigelow and Schroeder 1948, p. 451, following Garman 1913, p. 189) as alternative between *Centroscymnus,* where they are rounded on the type species at maturity (**coelolepis* Bocage and Capello 1864) and *Scymnodon,* where they are tridentate at maturity, is no longer tenable.

It seems appropriate here to recall that we owe to Steenstrup (1861) our knowledge that the dermal denticles of sharks do not persist throughout the life of the fish, growing as the latter grows, as the scales of bony fish do, but that they are constantly being shed, to be replaced by other, larger denticles. Thus several generations of denticles succeed one another during the life-span of any individual shark.

Fin spines. It seems worth emphasizing that the imbedded basal part of the fin spines is easily felt, in species in which their tips are concealed by the skin (p. 89).

Preoral clefts. The preoral clefts extend for about 40-50 per cent of the distance from the corner of the mouth toward the midline of the snout in **coelolepis* (incl. *cryptacanthus*) of the North Atlantic, in **owstoni* of Japan, and in *macracanthus* of the Magellanic region; about 60 per cent of that distance in *waitei* from New Zealand;[13] but for about 90 per cent of that distance in **crepidater* (incl. **jonsonii*) of the North Atlantic (Fig. 1D) and in *rossi* Alcock 1898 of the Indian Ocean (Alcock 1899, Pl. 26, fig. 3). Both **crepidater* and *rossi* fall, however, with the type species of *Centroscymnus* (**coelolepis*) in dental characters, in shape of pectoral fins, and in shortness of fin-

[12] The contour of the margins of the denticles is not known for *fuscus.*

[13] Taken from a drawing made available to us by Dr. J. A. F. Garrick before publication.

spines. Hence the difference in the length of the clefts does not call for generic recognition, especially where the total number of species concerned is so small.

Shape of caudal fin. Conditions in *Centroscymnus* argue against the presence or absence of a subterminal notch on the lower margin of the caudal as a subfamily alternative among the Squalidae, for while this notch is well marked in most of the members of the genus, it is indistinct in *waitei* (Garrick 1955, p. 233, fig. 1A). This seems the appropriate place for us to point out that the caudal of **coelolepis* is not correctly pictured in our earlier illustration (Bigelow and Schroeder 1948, fig. 94). Actually it is of the shape shown here on Figure 12 H.

Species. The following named species, listed in chronological order, are referable to *Centroscymnus* as defined here: **Centroscymnus coelolepis* Bocage and Capello 1864, type species, North Atlantic, east and west; **Centrophorus crepidater* (Bocage and Capello 1864), off Portugal; *Centrophorus rossi* Alcock 1898, Travancore Coast, India; *Centroscymnus cryptacanthus* Regan 1906, Madeira; *Centroscymnus macracanthus* Regan 1906, Magellanic region; **Centroscymnus owstoni* Garman 1906, Japan; *Centrophorus plunketi* (Waite) 1910, New Zealand (referred by Garman 1913, p. 210 and by Fowler 1941, p. 228 to *Scymnodon* because of its tridentate denticles); **Centrophorus jonsonii* (Saemundsson) 1922, Iceland; *Centroscymnus fuscus* Gilchrist and von Bonde 1924, southern Africa; *Centrophorus waitei* (Thompson) 1930, New Zealand.[14]

Detailed descriptions of the type species, **coelolepis*, with illustrations, have been given by Garman (1913, p. 204, Pl. 17, figs. 5-8), by Rey (1928, p. 451) and by Bigelow and Schroeder (1948, p. 494; 1954, p. 47). *Coelolepis* is known in the eastern Atlantic from the offing of Cape Verde and of Morocco to the Faroe Bank and to Iceland, including the western part of the Mediterranean; from the offing of Delaware Bay to the Banks of Newfoundland in the western. According to Regan's (1906, p. 437) account, his *cryptacanthus* from Madeira differs from the specimens of **coelolepis* that we have seen (including the one

[14] Our inclusion of *waitei* in *Centroscymnus* follows Garrick's (1955) study of the type specimen, the result of which was contributed to us by Dr. Garrick in advance of his publication.

on which Garman's illustration was based) in a slightly longer snout; in an interspace between the two dorsal fins about 6 times as long as the base of the first dorsal (4-5 times in *coelolepis*); in the extension rearward of the tips of the pelvic fins to abreast of the tip of the second dorsal fin; and in complete enclosure of the fin spines by the skin. Also, the denticles on the trunk rearward from abreast the first dorsal fin are described (Regan 1906, p. 437) as already rounded, and with concave crowns on a *cryptacanthus* only 700 mm. long (the type specimen), whereas various transitional stages are represented on a **coelolepis* of about that same size (690 mm., Bigelow and Schroeder 1954, p. 48, fig. 2). But with both **coelolepis* and *cryptacanthus* recorded from Madeira, the desirability is self-evident of comparison of the type of *cryptacanthus* (in the British Museum) with northern specimens of **coelolepis*.

**C. owstoni* from Japan (the type specimen of which is in the Museum of Comparative Zoology) differs from **coelolepis* of the Atlantic in a considerably longer snout, a somewhat larger eye, a considerably larger second dorsal fin relative to the size of the first dorsal, with the rear tip reaching more nearly to the upper origin of the caudal fin, and in relatively smaller — consequently more numerous — dermal denticles on the sides of the trunk.

The New Zealand shark that was described by Waite (1910) as *Centrophorus plunketi*, but which has been referred by Garman (1913 p. 210) to *Scymnodon*, and by Fowler (1933, p. 239; 1941, p. 228) to his subgenus *Proscymnodon*, is set apart from the *coelolepis-owstoni* pair by the tridentate shape of the denticles on the sides of the trunk on large specimens (type specimen a female 1414 mm. long) — presumably on small specimens also. And its denticles are both described and pictured (Waite 1910, p. 386, text fig.) as having as many as eight separate roots. The tips, also, of its pelvic fins are pictured (Waite 1909, Pl. 37) as reaching back only about as far as a perpendicular at the point of emergence of the second dorsal fin spine (they reach to a perpendicular at about the midpoint of the free lower margin of the second dorsal fin both in **coelolepis* and in **owstoni*), while the second dorsal fin is pictured as considerably larger in *plunketi* than it is either in **coelolepis* or in **owstoni*.

Dr. J. A. F. Garrick's study of the type specimen (a juvenile

male, 318 mm. long) of the shark described by Thompson (1930) as *Scymnodon waitei* places it definitely in the genus *Centroscymnus* as here defined, while his detailed account of it, with excellent illustrations, makes possible, for the first time, a satisfactory view of such of its characteristics as are the most evidently diagnostic of the species. Briefly, these are: snout in front of mouth shorter than distance from mouth to level of first gill openings; head, to origin of pectorals, about 20 per cent of total length; distance between inner ends of preoral clefts nearly or quite as long as between nostrils; base of second dorsal about twice (1.9) as long as base of first dorsal; dorsal fin spines with only the tips exposed; caudal fin without subterminal notch; dermal denticles on sides of body strongly tridentate, on four-angled base, and rising steeply from the skin; the outer exposed surface concave, without axial ridge; the denticles on the lower side of the snout ovate, with pointed tip and with prominent axial ridge. (For further details, including teeth, see Garrick 1955, pp. 233-238, figs. 1, 2.)

Thompson (1930, p. 278) followed by Richardson and Garrick (1953, p. 35) has suggested that *waitei* may prove to represent a stage in the growth of *Centroscymnus plunketi,* intermediate between the adult female that was the basis of Waite's original (1910) account of the latter, and the embryo, 165 mm. long, that was pictured subsequently by him (Waite 1914, p. 127, Pl. 3), from a litter of 36 taken from a female measuring 1398 mm. Solution of this question is, however, a matter for the future.

On the Magellanic shark named *C. macracanthus* by Regan (1906, p. 436), the dorsal fin spines (first as well as second, Fig. 12 E, F) project farther from the skin than they do in any of the other representatives of the genus discussed so far, though not as much as is suggested by Regan's (1906, p. 437) characterization of them as "strongly projecting." Its two dorsal fins also — especially the first — are larger relatively than in the specimens of **coelolepis* and of **owstoni* that we have seen, more nearly paralleling *plunketi* in this respect.[15] And the distance between the inner ends of its preoral clefts is nearly as long as

[15] We are indebted to Dr. Ethelwyn Trewavas and to Mr. Denys W. Tucker of the British Museum (Natural History) for tracings of the first and second dorsal fins, and to Dr. Ethelwyn Trewavas for the accompanying drawing of a lower tooth (Fig. 12 G), and for other details of the type specimen.

between the inner ends of the nostrils, to judge from Regan's (1906, p. 436) statement "length of anterior labial fold about equal to its distance from the symphysis." The flank denticles are tridentate on the type (and only known) specimen, but the latter is so small (640 mm. long, Regan 1906, p. 437) that this may represent a transitory state; those on mature specimens may be of a different shape, as they are in **C. coelolepis* (p. 87).

In the species of *Centroscymnus* so far mentioned, the gap between the inner ends of the preoral clefts is at least ¾ as long as the distance between the nostrils. In the three named species yet to be considered (**crepidater* and **jonsonii* of the northeastern Atlantic; *rossi* of the Indian Ocean) the clefts are so much longer that the space between their inner ends is only about one-third as long as between the nostrils (Figs. 1D, 12B). Other than this, the most sharply diagnostic features of **crepidater* are that its flank-denticles are tridentate on large specimens (Fig. 12D), as they also are in *C. plunketi* (p. 89), and that its first dorsal fin spine projects from the skin nearly as far as in *C. macracanthus* (cf. Fig. 12A with 12E, F).

The original (and only detailed) account of **C. jonsonii* (Saemundsson 1922, p. 192, Pl. 5) does not include any comparison with **crepidater,* nor does it suggest any definite ground for considering it as distinct from the latter. Comparison of seven specimens (male and female, 587-796 mm. long) from south of Iceland and southwest of the Faroes[16] with the 787 mm. female from Madeira (Fig. 12A), on which Günther (1870, p. 421) based his first-hand account of **crepidater,*[17] has revealed no significant differences, whether in teeth, in the shape of the denticles on large specimens, in bodily proportions (p. 93), or in the shapes, the sizes or the relative locations of fins. Consequently we have no hesitation in classing **jonsonii* as a synonym of **crepidater,* the known range of which extends (on this basis) from Madeira and the coast of Portugal northward to the Faroes and southern Iceland.

[16] Kindly made available to us by the Natural History Museum, Reykjavik, and by the University Zoological Museum, Copenhagen.

[17] We owe to the British Museum the opportunity to examine this specimen. Its identification as **crepidater* has been checked through correspondence with Dr. A. M. Ramalho, who has contributed measurements and photographs of the teeth of the type specimen which he has examined in Lisbon on our behalf.

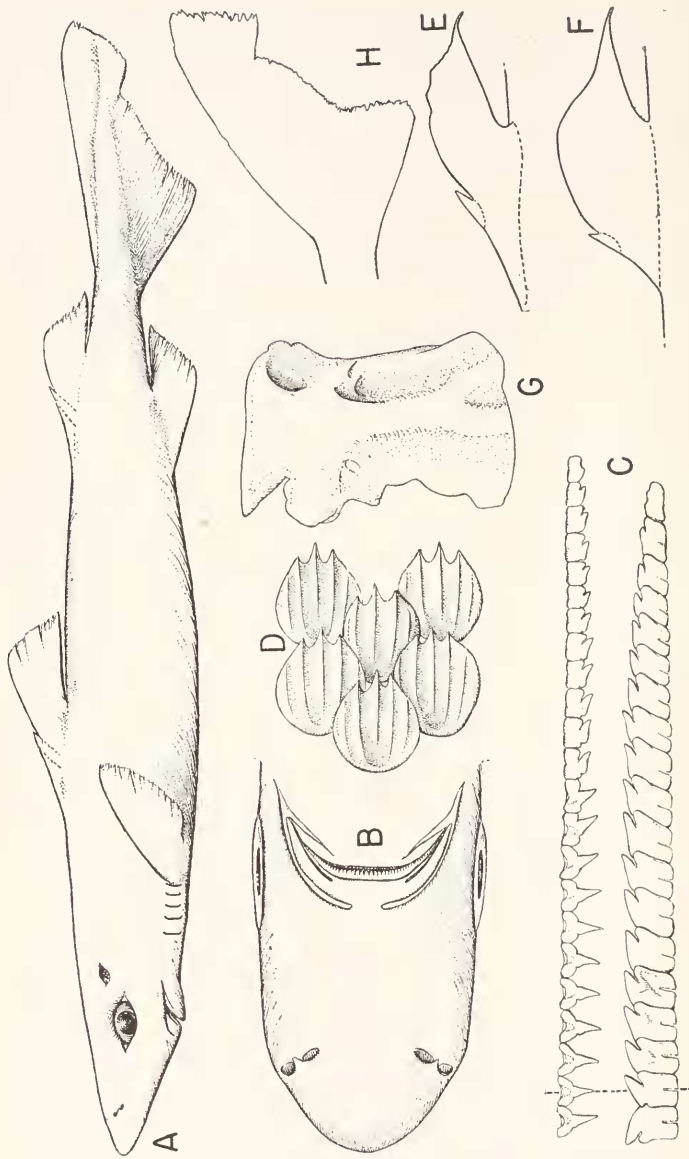

FIGURE 12

Dr. J. A. F. Garrick informs us, also,[18] that the Canterbury Museum contains two specimens of a shark taken on a long line set at 914 meters (500 fathoms) off Keikoura, New Zealand, and two others presumably from New Zealand but without definite locality, that differ from **crepidater* (including **jonsonii*) of the eastern North Atlantic only in such minor particulars that it is doubtful whether specific separation is warranted. And this we can corroborate, for we find no significant differences in bodily proportions, fins, teeth or denticles between one of these New Zealand specimens (kindly sent us by Dr. Garrick) and the Atlantic specimens that we have seen of **crepidater* (pp. 93-94).

Proportional dimensions in per cent of total length of **Centroscymnus crepidater*. A, female, 787 mm., Madeira, from the British Museum (Natural History); B, four females, 746 to 796 mm. long and C, male, 587 mm. long, off Iceland and the Faroes, from the University Zoological Museum, Copenhagen; D, female, 822 mm. long, presumably from New Zealand (see above), Mus. Comp. Zool. No. 39570.

Fig. 12. A, *Centroscymnus crepidater*, female, 787 mm. long, from Madeira, in British Museum. B, lower surface of head of same, to show the great length of the preoral clefts. C, upper and lower teeth of same, x about 2.3. D, denticles of same, from side below first dorsal fin, x about 6.5. E, *Centroscymnus macracanthus*, outline of first dorsal fin of a female, 640 mm. long, type specimen, in British Museum, from Magellanic region. F, outline of second dorsal fin of same; E and F, after tracings of the fins kindly contributed by Mr. Denys W. Tucker. G, third right hand lower tooth of same, x about 7, from drawing kindly contributed by Dr. Ethelwyn Trewavas. H, *Centroscymnus coelolepis*, caudal fin of female, 1035 mm. long, from offing of Delaware Bay, Mus. Comp. Zool. No. 38295.

[18] Information contributed by Dr. Garrick in advance of publication.

	A	B	C	D
Trunk at origin of pectoral: breadth	8.9	8.3-9.3	8.7	9.0
height	7.4	6.7-8.8	8.2	7.1
Snout in front of: eye	8.6	8.2-9.3	8.3	8.9
mouth	11.4	11.4-12.7	11.7	11.8
Eye: horizontal diameter	4.4	4.4-4.6	4.6	4.5
Mouth: breadth	6.1	6.1-7.5	7.5	7.1
Nostrils: distance between inner ends	3.3	3.1-3.6	3.2	3.6
Preoral clefts: distance between inner ends	1.1	1.1-1.3	1.0	0.7
Gill opening lengths: first	1.5	1.3-1.5	1.4	1.3
third	1.5	1.3-1.5	1.4	1.3
fifth	1.5	1.3-1.8	1.6	1.6
First dorsal fin: vertical height	5.2	5.1-5.5	5.4	4.6
length of base from origin of spine	7.5	5.9-6.7	7.0	6.6
Second dorsal fin: vertical height	4.8	4.3-5.9	5.4	5.0
length of base from origin of spine	7.1	6.3-6.8	7.0	7.3
Caudal fin: upper margin	22.2	19.0-20.7	20.8	18.9
lower anterior margin	13.2	10.7-13.5	13.0	13.4
Pectoral fin: width	5.3	5.2-6.8	4.2	5.2
length of anterior margin	13.1	11.8-13.1	11.4	12.4
Distance from snout to: first dorsal	28.9	28.1-30.5	30.7	29.2
second dorsal	60.2	61.0-64.2	60.3	61.7
upper caudal	77.8	79.3-81.5	79.2	81.1
pectoral	24.4	23.7-24.1	24.7	23.3
pelvics	60.6	61.0-65.0	56.3	62.2
Interspace between: origins of first and second dorsal spines	30.9	28.0-31.5	32.0	29.5
second dorsal and caudal	6.1	6.9-8.0	7.0	7.7
pelvics and caudal	8.0	7.4-8.8	10.0	7.9
Distance from origin to origin of:				
pectorals and pelvics	36.1	36.6-40.7	31.7	40.5
pelvics and caudal	15.8	15.2-17.9	17.9	15.7
Teeth, number of series: uppers	43	39-48	51	36+[19]
lowers	36	32 36	32	36+[19]

This adds to the list of cases among sharks and skates where a species, or pair of very closely allied species, is known from temperate latitudes in the two hemispheres, but not from the tropical-subtropical belt that intervenes.

C. rossi from the Indian Ocean, if represented correctly in Alcock's (1899, Pl. 26, Fig. 3) illustrations, differs from **crepidater* in a much longer head, and in detail as to the unpaired fins, especially the caudal which appears to lack the subterminal

[19] Several teeth have been lost at the corners of the mouth.

notch; perhaps also in the shapes of the teeth, though the illustrations of the latter by Alcock appear to be somewhat diagrammatic. The denticles on the sides of the trunk are strongly tridentate on juveniles (represented by the type specimen 254 mm. long), much as they are in **C. coelolepis* (Bigelow and Schroeder 1954, p. 48, Fig. 2B); the shape is not known for adults.

The relationship of *C. fuscus* of southern African waters to other members of its genus remains doubtful, for while it falls with **coelolepis* in length of snout, in the sizes and relative positions of fins, and in the concave crowns of the denticles on the sides of its body when mature (type and only known specimen 1,100 mm. long),[20] the length of its preoral clefts is not known. And the characterization of it in the original description (Gilchrist and von Bonde 1924, p. 2, our only source of information) as with orbits 1.7 times as long as the snout ("orbit .6 in snout") seems an obvious error, for this would credit it with eyes far larger than those of any related shark.

Key to Species of *Centroscymnus*

1. Distance between inner ends of preoral clefts at least 75 per cent as long as distance between nostrils 2
   Distance between inner ends of preoral clefts is not more than about 30 per cent as long as distance between nostrils C
2. Exposed part of first dorsal fin spine, measured along its anterior margin, is very nearly 50 per cent as long as distance from its point of emergence from the skin to rear end of base of the fin (Fig. 12F) ..
   macracanthus Regan 1906.
   Magellanic region. p. 90
   Dorsal fin spines exposed only at their extreme tips, if at all 3
3. Both of the dorsal fin spines are wholly concealed by the skin .....
   cryptacanthus Regan 1906.
   Madeira. p. 88
   The tips of the dorsal fin spines protrude more or less from the skin ..4
4. First dorsal fin, from point of emergence of spine to rear end of base, is about as long as second dorsal fin, similarly measured . **coelolepis*
   Bocage and Capello 1864.
   North Atlantic, east and west. p. 88
   First dorsal fin, from point of emergence of spine to rear end of base, is shorter than second dorsal fin, similarly measured 5

[20] Apparently the type specimen has been lost (Smith 1949, p. 58).

5. Snout in front of mouth is at least as long as from mouth to level of first gill openings ..... **owstoni* Garman 1906. Japan. p. 89

   Snout in front of mouth is noticeably shorter than from mouth to level of first gill openings ....*plunketi* Waite 1910. New Zealand. p. 89; also *waitei* Thompson 1930, New Zealand, perhaps a young stage of *plunketi* (see discussion, p. 90).

6. Head, to level of origin of pectoral fins, is only about 24-25 per cent of total length; caudal fin with distinct subterminal notch ..... **crepidater* Bocage and Capello 1864, including **jonsonii* Saemundsson 1922. Eastern North Atlantic. p. 91; also New Zealand, or represented there by a close ally (see discussion, p. 93).

   Head to level of origin of pectoral fins about 31 per cent of total length, caudal fin without distinct subterminal notch ..... *rossi* Alcock 1898. Indian Ocean. p. 94

   Systematic position in the genus doubtful ..... *fuscus* Gilchrist and von Bonde 1924. Southern Africa, see discussion, p. 95.

Genus SCYMNODON Bocage and Capello 1864

Scymnodon Bocage and Capello 1864, p. 263; 1866, p. 31, type species **S. ringens* Bocage and Capello 1864, p. 263; 1866, p. 32, Pl. 1, fig. 1; Pl. 3, fig. 2A; type locality off Portugal.

Generic Synonyms:

Centrophorus in part, Günther 1870, p. 423, for **Scymnodon ringens* Bocage and Capello 1864.

Zameus Jordan and Fowler 1903, type species *Centrophorus squamulosus* Günther 1877, Japan.

Not *Centrophorus* Müller and Henle 1837, type species **Squalus granulosus* Bloch and Schneider 1801.

Generic characters. As in *Centroscymnus* (p. 85), except with the upper teeth much longer midway along each side of jaw than either toward the center of the mouth or toward its outer corners (Fig. 13C). Lower teeth triangular, highest and symmetrical along median sector of jaw, shorter but only weakly

oblique toward outer corners of mouth; first and second dorsal fin spines scarcely projecting beyond the skin; dermal denticles on sides of trunk scale-like, tridentate, the outer surface with longitudinal ridges alone in some species, including the type but also with cross ridges (Fig. 13, F, G) in one species (*obscurus* Vaillant 1888) that seems referable to *Scymnodon* by its dentition.

Maximum recorded length 1100 mm. for *ringens* (Bocage and Capello 1866, p. 32).

Depth range. One of the four known representatives of this genus has been reported from a depth as great as 1400-1435 meters (one specimen, Vaillant 1888, p. 68); a second, *squamulosus* (Günther 1887, p. 6), from 631 meters. A young specimen, however (the only one known) of a third was found on the beach at North Brighton, New Zealand (Archey 1921, p. 195). No information in this respect is at hand for the type species of the genus, so far known only from Portugal and from the northern coast of Spain (Rey 1928, p. 457).

Remarks. Günther (1870, p. 420) thought that "the passage . . . from reclining to erect teeth in the lower" jaw is too gradual to justify the separation of *Scymnodon* from *Centroscymnus;* or the separation of either of these from *Centrophorus,* for that matter. But the difference in dentition between the species referred here to *Scymnodon* and those referred to *Centroscymnus* (p. 88) is in fact so conspicuous that a glance at the mouth is enough to place a given specimen in the one category or in the other (provided it is properly referable to either), which makes the retention of *Scymnodon* as a separate genus a matter of convenience, even if nothing more.

The contrast is also interesting between the pointed or tridentate denticles, with longitudinal ridges, on the sides of the trunk on mature specimens of *Scymnodon* and the replacement of denticles of this type by evenly rounded ones with concave blades, in some of the species of *Centroscymnus* (p. 86). But this difference can no longer be regarded as alternative between the two genera, for the denticles are tridentate in the adults of two of the species (**crepidater* Bocage and Capello 1864, and *plunketi* Waite 1909), the teeth of which place them in *Centroscymnus* (p. 88). In any case choice of the denticles rather than of the dentition as the primary distinction between *Scym-*

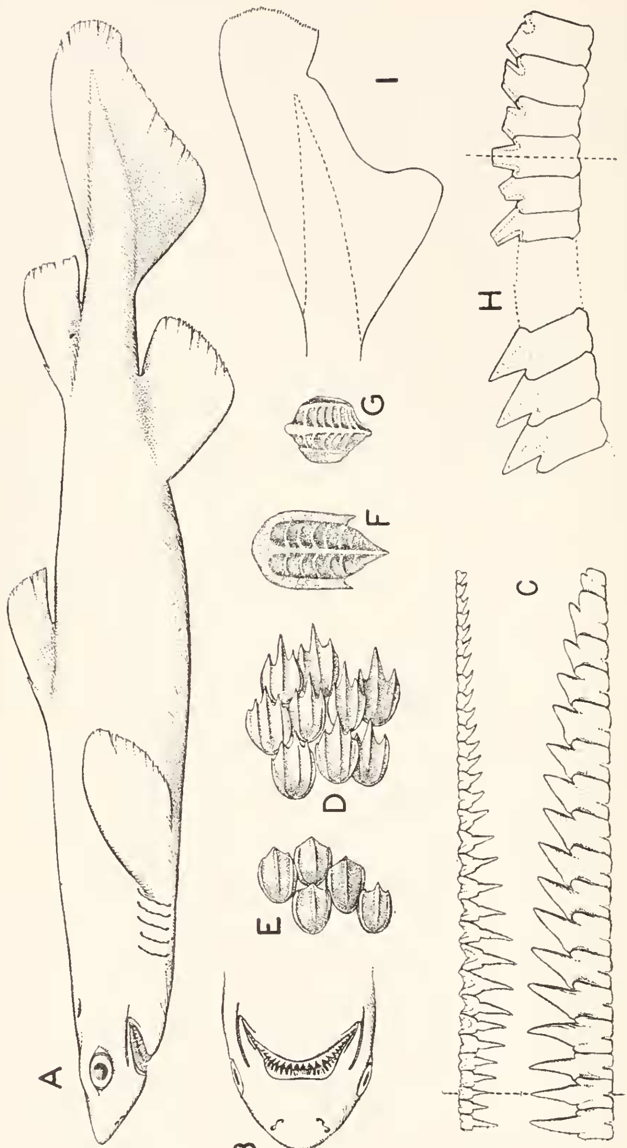

FIGURE 13

nodon and *Centroscymnus,* as by Garman (1913), by Fowler (1941), and by Bigelow and Schroeder (1948) would provide no basis on which to refer a given specimen to the one genus rather than to the other, unless it chanced to be full grown or nearly so. While the only illustration of one of the three known species of *Scymnodon* (*squamulosus* Günther 1877) shows no sign of fin spines, the artist seems to have overlooked them, for Günther (1887, p. 6, Pl. 2, Fig. B) wrote of them as "very small, scarcely projecting beyond the skin."

Species: Named species referable to *Scymnodon* as defined here are: **S. ringens* Bocage and Capello 1864, type species, offing of Portugal; *Centrophorus squamulosus* Günther 1877, Japan; and *Centroscymnus obscurus* Vaillant 1888, off the coast of northwestern Africa,[21] in a haul from 1400-1435 meters. The New Zealand shark, also, that was described by Archey (1921) as *Scymnodon sherwoodi* has been retained in that genus by the several authors (Whitley 1934, 1940; Fowler 1941; Bigelow, Schroeder and Springer 1953; and Richardson and Garrick 1953), who have had occasion to refer to it. But we now learn from Dr. J. A. F. Garrick[22] that the type (and only known) specimen, which he has recently examined, shows no trace of a spine in either of its dorsal fins, and that it is therefore one

Fig. 13. A, *Scymnodon ringens,* female, 893 mm.. long, coast of Portugal, in British Museum. B, ventral view of anterior part of head of same. C, upper and lower teeth of same, left hand side of mouth, x about 1, midpoint of jaws marked by the dotted line. D, dermal denticles of same, from side below first dorsal fin, x about 7. E, dermal denticles of same from side of caudal peduncle x about 7. F, *Scymnodon obscurus,* dermal denticle of type specimen, female, 590 mm. long, off northwest Africa (p. 100), from side below first dorsal fin, x about 18, made available to us through kindness of Dr. P. Budker. G, dermal denticle of same, after Vaillant, 1888, Pl. 2, Fig. 2. H, lower teeth of same, from drawing contributed by Dr. P. Budker, x about 4. I, *Scymnodon squamulosus,* type specimen, female, 658 mm. long, Japan, in British Museum, outline of caudal fin from drawing contributed by Mr. Denys W. Tucker.

[21] The locality as given by Vaillant (1888, p. 68), is "sur les côtes du Soudan," a designation referring to the general region from southern Morocco to Senegal (Folin, 1887, pp. 287-300).

[22] Information contributed by Dr. Garrick in advance of publication.

of the Dalatiinae not of the Squalinae, as the sub-families are defined here (p. 18).

We have pointed out elsewhere (Bigelow and Schroeder 1954, p. 51) that the juvenile shark from the northwestern Atlantic, on which Bigelow, Schroeder and Springer (1953, p. 233) based their new species **Scymnodon melas,* actually represented a juvenile stage in the growth of **Centroscymnus coelolepis* Bocage and Capello 1864.

The dentition of *obscurus* closely resembles that of **ringens,* as Dr. Paul Budker has kindly verified for us from examination of the type specimen of *obscurus* in the Paris Museum. Indeed, Garman (1913, p. 208) has definitely rated *obscurus* as a synonym of **ringens.* But a more abruptly truncate caudal fin, with more definite subterminal notch and smaller pectorals in *obscurus* (as pictured by Vaillant 1888, Pl. 2, Fig. 2) than in **ringens,* and flank denticles with a double series of transverse ridges between the more prominent longitudinal ridges (Fig. 13, F, G; see also Vaillant 1888, Pl. 2, Fig. 2C) argue against this union, hence *obscurus* is retained here as a distinct species. It is interesting, also, that in *obscurus* some of the denticles on the sides of the trunk of a given individual may be tridentate, while others are not (Fig. 13, F, G).

The Japanese *squamulosus* (Günther 1887, p. 5, Pl. 2, Fig. B) agrees with **ringens* in the shape of its denticles. But an examination of the type specimen in the British Museum by Mr. Denys W. Tucker (to whom we are greatly indebted), shows its gill openings as only about 50 per cent as long, relatively, as those of **ringens;* its snout as longer relatively and more pointed (length from tip of snout to mouth about as great as distance between inner ends of preoral clefts); and both its second dorsal, its pectoral and ventral fins, also its caudal (Fig. 13, I), as differing so conspicuously from those of **ringens,* that the two species are clearly distinct. In all these respects, indeed, *squamulosus* so nearly resembles *obscurus* (as pictured by Vaillant 1888, Pl. 2, Fig. 2) that these two species might easily be confused. But the denticles on the sides of the trunk of *squamulosus* (as pictured by Günther 1887, Pl. 2, fig. B) show no trace of the transverse ridges that mark the denticles of *obscurus* (Fig. 13, F, G).

Key to Species of *Scymnodon*

1. Lower outline of caudal fin nearly continuously rounded, with subterminal notch only faintly marked, and without definite lower-anterior lobe (Fig. 13A); pectoral fin, when laid back, reaching very nearly to a perpendicular at base of first dorsal fin spine ..... **ringens* Bocage and Capello 1864, eastern North Atlantic. p. 99

   Lower outline of caudal fin with well-marked subterminal notch and prominent lower anterior lobe (Fig. 13, I); pectoral fin, when laid back, falls short of a perpendicular at base of first dorsal fin spine by a distance at least 50 per cent as long as snout anterior to eyes 2

2. Outer surface of dermal denticles on sides of trunk with weak transverse ridges in addition to the three longitudinal ridges (Fig. 13, F, G). ..... *obscurus* Vaillant 1888, off coast of Northwestern Africa. p. 100

   Outer surface of dermal denticles on sides of trunk without transverse ridges ..... *squamulosus* Günther 1877, Japan. p. 100

Genus DEANIA Jordan and Snyder 1902

Deania Jordan and Snyder 1902, p. 80, type species, **D. eglantina* Jordan and Snyder, Japan.

Generic Synonyms:

Acanthidium in part, Lowe, 1839, p. 92, for **A. calceum* Lowe, Madeira.

Centrophorus in part, Lowe, 1843, p. 93, and subsequent authors, for *C. calceus* Lowe 1843, equals **Acanthidium calceum* Lowe 1839.

Centrophorus in part, Bocage and Capello 1864, 1866, for *C. crepidalbus* Bocage and Capello, evidently equals **Acanthidium calceum* Lowe 1839.

Scymnodon in part, Goode and Bean 1895, by error, their Pl. 4, Fig. 12, labelled "*S. ringens* Bocage and Capello" in the explanation of plates being a copy of the illustration by Bocage and Capello (1866, Pl. 2, Fig. 1) of *Centrophorus crepidalbus* Bocage and Capello 1864, equals *Acanthidium calceum* Lowe 1839.

Nasisqualus Smith and Radcliffe 1912, p. 681, type species **N. profundorum* Smith and Radcliffe, Philippines.

Acanthidium Garman 1913, p. 215; type designated as **A. calceum* Lowe 1839; but incorrectly so, because **A. pusillum* Lowe 1839 (which is a species of *Etmopterus* Rafinesque 1810, see below) had previously been designated as the type of *Acanthidium* by Jordan and Evermann (1896, p. 55).

Daeniops Whitley 1932, p. 36, type species *Acanthidium quadrispinosum* McCulloch 1915, Australia.

Not *Centrophorus* Müller and Henle 1837, type species **Squalus granulosus* Bloch and Schneider 1801.

Not *Acanthidium* Lowe 1839, type species **A. pusillum* Lowe as designated by Jordan and Evermann 1896, p. 55, and by Jordan 1919, p. 195, making *Acanthidium* a synonym of *Etmopterus* Rafinesque 1810 (see above).

Not *Scymnodon* Bocage and Capello 1864, 1866, type species **S. ringens* Bocage and Capello 1864.

Generic characters. Inner corner of pectoral fins rounded in most species, perhaps rectangular in some, but not extended (p. 103); snout in front of mouth longer than from mouth to level of origin of pectoral fins; preoral clefts only very slightly expanded inwardly; dermal denticles on sides of trunk high, pitchfork shaped; teeth smooth-edged in all known species; other characters as in *Centrophorus* (p. 64).

Maximum recorded lengths, 1138 mm. (*quadrispinosa* McCulloch 1915, p. 100); 1070 mm. (*kaikourae* Thompson 1930, as "*calceus*"); and 1060 mm. (*calcea,* Vaillant 1888, p. 71).

Depth range. The depths of capture so far recorded for *Deania* (mostly, at least, in the trawl, hence subject to the uncertainty emphasized on p. 5) are: 605-1431 meters for *calcea* (Roule 1919, p. 119); 715-1785 meters for **profundorum* (Smith and Radcliffe 1912, p. 683); 190-366 meters for **eglantina* (Smith 1949, p. 58); and 238-823 meters for *quadrispinosa* (McCulloch 1915, p. 100; Whitley 1940, p. 147). While definite information as to depth is wanting for *kaikourae,* it was reported from "deep water" (Thompson 1930, p. 276, as "*calceus*"). And the Japanese records for **aciculata* (Garman) 1906, **rostrata* Garman 1906, and *hystricosa* (Garman) 1906 which we here refer to **eglantina* (p. 104) were from the deep line-fishery in Sagami Bay. Evidently *Deania* can fairly be termed a deep-water genus.

Remarks. The chief respects in which the various species that have been grouped together as *Deania* (or as one or other of its synonyms) differ from *Centrophorus* are: a much longer snout, and pitchfork-shaped denticles on the sides of the body. Most of the species of *Deania* are set further apart from *Centrophorus* by the rounded shape of the inner corner of their pectoral fins. But the two genera intergrade in this respect, the inner corner of the pectorals being quadrate, both in one member of *Centrophorus* (*foliaceus* Günther 1877), as noted above (p. 66), and

also in one member of *Deania*, if Gilchrist's (1922, Pl. 7, Fig. 2) illustration of his *D. natalense* represents the latter correctly.[23]

Deania differs from *Centroscymnus* and from *Scymnodon* in a much longer snout; in a longer exposed portion of the second dorsal fin spine; and in broader upper teeth. It differs further from *Scymnodon* in that the teeth in the central part of its upper jaw are nearly or quite as long as those midway out along either side. It had appeared also until recently that its high, pitchfork-shaped denticles were equally diagnostic of *Deania* as contrasted with *Centrophorus* and with the *Centroscymnus-Scymnodon* group. But Garrick (1955, p. 234, Fig. 2) has found that the denticles on the sides of the trunk of young specimens of *Centroscymnus waitei* (Thompson) 1930 of New Zealand (p. 90) approach the pitchfork-like shape that was formerly thought to be diagnostic of the denticles of *Deania*.

The cusps of the upper teeth of *Deania* are sharp-tipped, rather narrowly triangular, with concave margins, on broad bases;[24] erect along the central part of the jaw, but increasingly oblique toward the outer corners of the mouth.

The lower teeth are very strongly oblique all along either side, and the median tooth is not symmetrical in the female of any species for which the condition in this respect is known. In **calcea* (Lowe) 1839 (the oldest species), the lowers are of the same shape in the males as in the females, as illustrated by a male of 848 mm. and a female of 1037 mm. that we have seen from southwest of the Faroes.[25] Similarly, the lowers are described and pictured as strongly oblique in the male in **profundorum* (Smith and Radcliffe 1912, p. 681, Pl. 53), which we can verify from our examination of the type specimen. But the lowers are described by McCulloch (1915, p. 101) as much less strongly oblique in the males of *quadrispinosa*, from Australia, than in the females, which is also the case in the Japanese species-complex that we unite here (p. 104) under the name **eglantina* Jordan and Snyder 1902. Thus the lowers (including the median tooth) of the female pictured by Garman

[23] The pectoral fins are not mentioned in Gilchrist's (1922, p. 49) description of his *natalense*.

[24] Our re-examination of the type specimen of **Deania eglantina* (type of the genus) has shown that Jordan and Snyder's (1902, p. 81) description of the teeth as with "small basal cusp" is not correct.

[25] We are indebted to Dr. J. R. Pfaff, of the University Zoological Museum, Copenhagen, for the opportunity of seeing these specimens.

(1913, Pl. 11, Fig. 7) as *Acanthidium hystricosum*[26] are shown as strongly oblique, whereas those of the adult male figured by him (Garman 1913, Pl. 12, Fig. 2) as **Acanthidium aciculatum* (which we have examined) are erect in the front of the mouth, with the median tooth symmetrical. And the reserve rows of lower teeth of an immature male, 682 mm. long, in the Museum of Comparative Zoology, are similarly nearly erect along the center of the jaws (the functional row is badly worn). The situation in this respect is not known for *natalense* or for *kaikourae*.

It is a matter of common knowledge that sexual dimorphism of this sort is common among batoid elasmobranchs, but it seems not to have been reported previously among sharks.

Species: Named species referable to *Deania:* are **Acanthidium calceum* Lowe, 1839, eastern Atlantic; **Deania eglantina* Jordan and Snyder 1902, type species, Japan; **Acanthidium aciculatum* Garman 1906, *A. hystricosum* Garman 1906, and **A. rostratum* Garman 1906, all from Japan; **Nasisqualus profundorum* Smith and Radcliffe 1912, Philippines; *Acanthidium quadrispinosum* McCulloch 1915, Australia; *Acanthidium natalense* Gilchrist 1922, Natal, southeastern Africa; and *Centrophorus kaikourae* Whitley 1934, New Zealand, which was originally reported and pictured by Thompson (1930, p. 275, Pl. 42 as *Centrophorus calceus* Lowe).

Our re-examination of the type specimens of **eglantina* (a female of 300 mm.), **aciculata* (a male of 890 mm.) and **rostrata* (a female of 873 mm.) has revealed no differences between them in proportional dimensions (see below) greater than may reasonably be credited to the difference between them in stage of growth, or to the variability that has already been reported by Regan (1908, p. 52) for the allied **calcea* of the Atlantic. Cases in point are the somewhat longer head and caudal fin, but shorter interdorsal space of the **eglantina*. And while the type specimen of the fourth member of this group (*hystricosa*) is no longer to be found, Garman's (1913, Pl. 11, Figs. 5-8) beautiful illustrations of it, by the well-known zoological artist E. N. Fischer, do not suggest anything to set it apart either. Hence, all deanias yet reported from Japan are referred here to the one species **eglantina* Jordan and Snyder 1902.

[26] This specimen is no longer to be found.

Proportional dimensions in per cent of total length. A. **Deania eglantina,* female, 300 mm., type, U.S.N.M. No. 49524; B. **D. rostrata,* female, 873 mm., type, M.C.Z. No. 1047; C. **D. aciculata,* male 890 mm., type, M.C.Z. No. 1128; all from Japan.

	A	B	C
Trunk at origin of pectoral: breadth	9.3	7.5	6.7
height	7.7	8.0	6.7
Snout in front of: outer nostrils	5.3	5.3	4.0
mouth opening	15.3	13.7	12.1
Eye: horizontal diameter	5.3	3.6	4.7
Mouth: breadth	7.7	5.6	6.4
Nostrils: distance between inner ends	4.5	3.4	3.4
Preoral clefts: distance between inner ends	4.8	3.4	3.7
Gill opening lengths: first	2.0	—	1.7
third	2.0	2.5	1.7
fifth	2.0	2.1	1.8
First dorsal fin: vertical height	3.8	3.5	2.9
length of base from spine origin	9.5	9.7	11.8
Second dorsal fin: vertical height	4.7	5.5	4.8
length of base from spine origin	9.2	10.0	10.0
Caudal fin: upper margin	20.0	16.0	16.8
lower anterior margin	11.6	10.8	9.8
Pectoral fin: width	6.2	6.1	6.1
length of anterior margin	9.3	9.0	8.9
Distance from snout to: 1st dorsal spine	42.3	39.9	40.2
2nd dorsal spine	68.2	70.5	70.5
upper caudal	80.0	84.0	83.2
pectoral	28.7	24.0	23.2
pelvics	61.6	64.7	62.6
Interspace between: origins of first and second dorsal spines, at base	24.6	30.5	30.7
second dorsal and caudal	3.8	3.2	3.4
pelvics and caudal	8.9	10.3	10.1
Distance from origin to origin of:			
pectorals and pelvics	33.3	40.8	39.3
pelvics and caudal	13.3	13.4	14.4
Teeth, number of series: uppers	28	34	29
lowers	13-1-14	?	29

The Japanese **eglantina* (including Garman's supposedly distinct species, as just noted), is so closely allied to **Deania calcea* of the eastern Atlantic that Regan (1908, p. 51) has already relegated it unequivocally to the synonymy of **calcea,* and

**aciculata* doubtfully so. But it seems to us wiser to retain **eglantina* as a separate species, at least until a large number of specimens of the Japanese and North Atlantic populations have been studied, for while the Japanese specimens listed above agree very closely indeed with the two **calcea* we have seen, in fin characters and in bodily proportions in general, the lower teeth are as oblique in the males of **calcea* as in the females, but are more erect in mature males than in females in **eglantina,* as noted above (p. 103). Though this last difference would not be an aid to identification unless the species in hand chanced to be well-grown males, it deserves taxonomic recognition of some sort. And the question as to whether the North Atlantic and North Pacific populations of this general type have diverged significantly since they became isolated geographically, one from the other, is one too interesting to be answered offhand.

The **calcea-*eglantina* group of the Northern Hemisphere has close counterparts, in the Southern Hemisphere, in *quadrispinosa* of Australia; also in a shark reported and pictured from southern African waters by Smith (1949, p. 58, Fig. 49) as **eglantina,* which certainly resembles the type specimen of **eglantina* very closely. But the eventual decision as to the identity of either or both of these with **eglantina* of Japan must await the comparison of specimens from the different ocean areas.

In the **calcea-*eglantina-quadrispinosa* group (however many species this may eventually prove to represent), the pectoral fins, when laid back, fall considerably short of a vertical at the point of emergence from the skin of the first dorsal fin spine. But the pectorals of **profundorum* from the Philippines are pictured as reaching rearward to abreast of the first dorsal spine (Smith and Radcliffe, 1912, Pl. 53), and our own examination of the type specimen has shown this to be correct. As this is a rather conspicuous difference, **profundorum* may be accepted as a good species.

The original illustration of *natalense* (Gilchrist 1922, Pl. 7, Fig. 2) of southern African waters, shows the pectorals not only as reaching rearward beyond the first dorsal spine, but also with the inner corner quadrate, instead of rounded as they are in other known representatives of the genus *Deania.* But Smith's (1949, p. 58) allocation of it (with *quadrispinosa*) to the synonymy of **eglantina* — perhaps from examination of the type

which Barnard (1925, p. 51) has reported as being in the collection of the Government Marine Survey of South Africa — suggests that the artist's representation of *natalense* may not have been correct. Hence its status remains in doubt, pending further information.

Finally, *kaikourae* (falling with the **calcea*-**eglantina* group in length of pectoral fin) differs from all other known members of *Deania* in a first dorsal fin base about 1.6 times as long as the second (each measured from the point of emergence of the respective fin spine from the skin), contrasted with 0.9-1.2 times for the **calcea*-**eglantina-quadrispinosa* group, for **profundorum*, and for *natalense*. Thompson (1930, p. 276) indeed, has already called attention to this feature in his original account of *kaikourae* (as "*Centrophorus calceus*").

To sum up, the nine representatives of the genus *Deania* that have been named from various seas may represent as few as four species, **calcea* in the North Atlantic, **eglantina* in the North and South Pacific and southern Indian Ocean, *kaikourae* from New Zealand, and **profundorum* in Philippine waters. Or they may represent as many as six, if *quadrispinosa* from Australia, and the South African form reported by Gilchrist 1922 as *natalense*, but by Smith (1949) as **eglantina*, should finally prove to be separable, not only from **eglantina* of the North Pacific, but one from the other as well.

Key to Species of *Deania*

1. Pectorals, when laid back, falling considerably short of a perpendicular at point of emergence of first dorsal fin spine from the skin 2
   Pectorals, when laid back, reach at least as far as a perpendicular at point of emergence of first dorsal fin spine 4
2. First dorsal fin, from point of emergence of spine to rear end of base is 1.5-1.6 times as long as second dorsal, similarly measured .....
   kaikourae Whitley 1934, Australia. p. 107
   First dorsal fin, from point of emergence of fin spine to rear end of base of fin, is only 0.9-1.2 times as long as second dorsal fin, similarly measured 3
3. Lower teeth as strongly oblique in males as in females .....
   **calcea* Lowe 1939.
   Northeastern Atlantic, including Mediterranean, p. 105
   Lower teeth more erect in males than in females .....**eglantina*

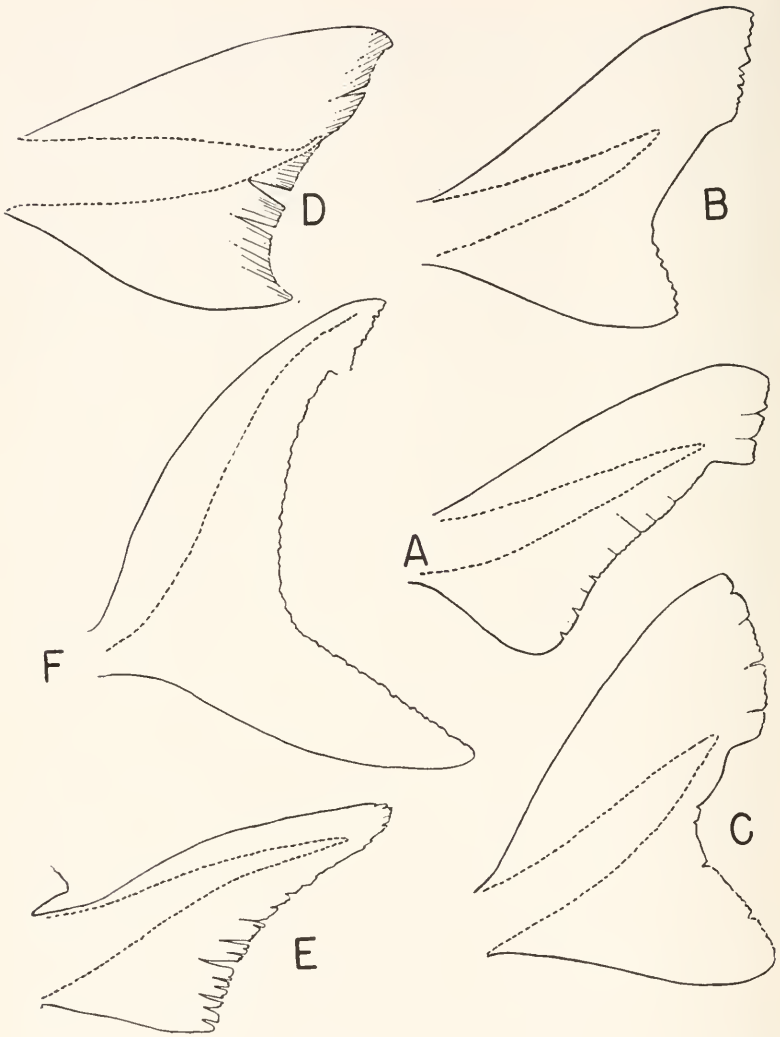

FIGURE 14

Jordan and Snyder 1902 (incl. **aciculata* Garman 1906, **rostrata* Garman 1906, and *hystricosa* Garman 1906), Japan, and reported from southern Africa (p. 106); also *quadrispinosa* Gilchrist 1922, Australia. p. 106

4. Inner corner of pectoral fins rounded; first dorsal fin only about 70 per cent as high vertically as second dorsal fin ..... **profundorum* Smith and Radcliffe 1912, Philippines. p. 106

Inner corner of pectoral fins quadrate; first dorsal fin about as high vertically as second dorsal fin ..... *natalense* Gilchrist 1922. Off Natal coast, southern Africa (but see discussion). p. 107

Subfamily DALATIINAE

Subfamily characters. Squalidae lacking a second dorsal fin spine (lacking a first spine also in most cases); preoral clefts lacking in most but present in one of the known genera (*Scymnodalatias*, p. 124); dermal denticles either truncate with hollow crown, or with a single cusp or spine; teeth with only one cusp, the uppers narrow, awl shaped or lancet shaped; the lowers much broader, with quadrate base, each overlapping the next outward; caudal axis raised in some but not in others; the caudal fin varying widely in shape accordingly (Fig. 14), its tip more or less evidently truncate; sides of body, anterior to cloaca, without longitudinal ridges.

Fig. 14. Outlines of caudal fins of representative genera, adjusted to equal lengths along upper margin, to show relative breadth of fin above axis and below; also degree to which caudal axis is raised. A, *Dalatias licha*, male, 1114 mm. long, Japan, Mus. Comp. Zool. No. 1116. B, *Somniosus microcephalus*, male, 1334 mm. long, Massachusetts Bay, Mus. Comp. Zool. No. 39609. C, *Isistius brasiliensis*, male, 383 mm. long, western North Atlantic north of the Bahamas, Mus. Comp. Zool. No. 36039. D, *Squaliolus laticaudus*, same specimen as in Fig. 16A. E, *Echinorhinus brucus*, male, 1650 mm. long, Mauritanian coast, northwest Africa, Mus. Comp. Zool. No. 39633. F, *Lamna ditropis*, type specimen, male, 2085 mm. long, off La Jolla, California, Mus. Comp. Zool. No. 36471, the vertebral axis indicated by the broken line.

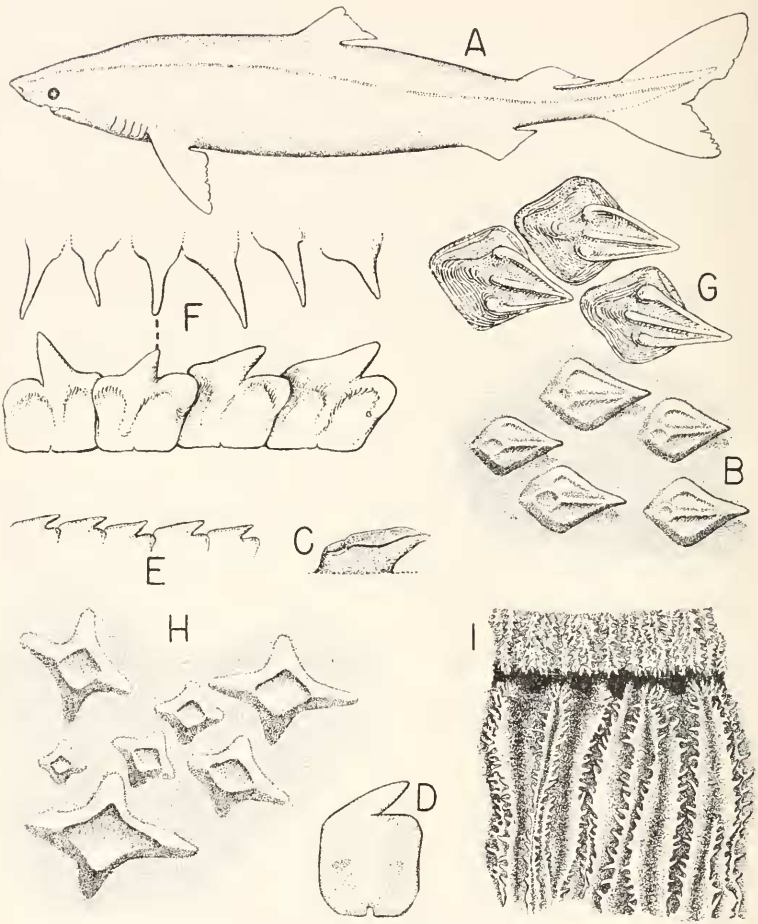

FIGURE 15

Genera. The shark species referable to this admittedly "artificial" group have been distributed among the following named genera: (1) *Dalatias* Rafinesque 1810, type species *D. sparophagus* Rafinesque, equals **Squalus licha* Bonnaterre 1788; (2) *Somniosus* Lesueur 1818, type species *S. brevipinna* Lesueur, equals **Squalus microcephalus* Bloch and Schneider 1801; (3) *Euprotomicrus* Gill 1864, type species *Scymnus* (*Laemargus*) *labordii* Müller and Henle 1841, equals **Scymnus bispinatus* Quoy and Gaimard 1824; (4) *Isistius* Gill 1864, type species **Scymnus brasiliensis* Quoy and Gaimard 1824; (5) *Heteroscymnus* Tanaka 1912, type species **H. longus* Tanaka; (6) *Squaliolus* Smith and Radcliffe 1912, type species **S. longicaudus* Smith and Radcliffe; (7) *Heteroscymnoides* Fowler 1934, type species **H. marleyi* Fowler; (8) *Pseudoscymnus* Herre 1935, type species *P. boshuensis* Herre; and (9) *Scymnodalatias* Garrick 1956, type species *Scymnodon sherwoodi* Archey 1921. There seems nothing, however, to set *Pseudoscymnus* apart from *Dalatias* (Bigelow and Schroeder 1948, pp. 501, 502). And Hubbs and McHugh's (1951, p. 164, Footnote) suggestion that *Heteroscymnus* should be reduced "perhaps to the synonymy of *Somniosus,*" is supported by our examination of the teeth (Pl. 3) and denticles (Fig. 15B) of the one known species, **H. longus* Tanaka 1912, from Japan. For further discussion of it see page 121.

Fig. 15. A, *Somniosus longus,* type specimen, female, 1360 mm. long, Japan, after Tanaka, the shapes of the fins somewhat emended to accord with a Japanese male, 1010 mm. long, Mus. Comp. Zool. No. 39650, kindly contributed by Dr. Tokiharu Abe. B, dermal denticles of latter, from side below first dorsal fin, x about 25. C, side view of same. D, *Somniosus rostratus,* lower tooth of Mediterranean female, 820 mm. long, after Canestrini, 1864, Pl. 2, Fig. 4. E, lower teeth near center of jaw, of Portuguese shark described by Capello 1870 under the name "*rostratus*", traced from a photograph contributed by Dr. A. M. Ramalho. F, *Heteroscymnoides marleyi,* type specimen (see Fig. 16E), upper and lower teeth at center of mouth, x about 12. G, dermal denticles of same, from side below first dorsal fin, x 36. H, *Squaliolus laticaudus,* same specimen as in Figure 16A, denticles on side below first dorsal fin, x about 45. I, *Dalatias licha,* same specimen as in Figure 14A, a sector of the exposed part of upper and lower lips, x about 4.

In short, the dozen or so known species of Dalatiinae that appear to deserve separate recognition seem referable to 6 or 7 genera as defined by the positions and relative sizes of the first and second dorsal fins, presence or absence of a spine on the first dorsal fin, nature of the teeth, shape of the dermal denticles on the sides of the body, and degree to which the portion of the caudal fin above the axis is developed relative to the portion below the axis. This last matter is one of especial interest, as already stressed by Hubbs and McHugh (1951, p. 164) in their key to genera, for in the genera in which the fin is the most widely expanded above the axis (Fig. 14), the latter is raised only very slightly above the main axis of the shark's body (if at all). In other words, one of the evolutionary trends of the group has been a tendency for the tail to lose the heterocercal nature so characteristic for it among sharks in general. Caudal fins even more lunate in form (Fig. 14F) are, it is true, well known characteristics of the isurid, basking, and whale sharks. But in all of these the caudal axis is steeply raised; they are, in a word, as truly heterocercal as any other shark, more noticeably so, indeed, than many, such as the erectolobids, scyliorhinids and some of the triakids.

Key to Genera of Dalatiinae

1. Lips with a complex series of fringed cross folds (Fig. 15, I); margins of lower teeth regularly serrate ..... *Dalatias* Rafinesque 1810. p. 113
   Lips smooth, or nearly so; margins of lower teeth smooth, or only faintly and partially serrate at most 2
2. First dorsal fin with a spine, the tip either exposed or buried in the skin ..... *Squaliolus* Smith and Radcliffe 1912. p. 128
   First dorsal fin with no trace of a spine 3
3. Preoral clefts present; upper margin of caudal fin about twice as long as lower anterior margin ..... *Scymnodalatias* Garrick 1956. p. 124
   No preoral clefts; upper margin of caudal fin not more than 1.5-1.7 times as long as lower anterior margin, and relatively shorter than this in most 4
4. Rear end of base of first dorsal fin is over or posterior to origin of pelvic fins; interspace between first and second dorsal fins is shorter than between second dorsal fin and origin of upper margin of caudal; lower teeth erect, symmetrical ..... *Isistius* Gill 1864. p. 123

Rear end of base of first dorsal fin is clearly anterior to origin of pelvics; interspace between first and second dorsal fins is at least as long as between second dorsal fin and origin of upper side of caudal; lower teeth asymmetrical, the cusp more or less strongly oblique, outward 5

5. Origin of first dorsal fin is about over axil of pectorals ..... *Heteroscymnoides* Fowler 1934. p. 182

Origin of first dorsal fin is posterior to tips of pectorals when these are laid back 6

6. Base of first dorsal fin about as long as base of second dorsal; eye only about 20-25 per cent as long as snout in front of mouth ..... *Somniosus* Lesueur 1818. p. 115

Base of first dorsal fin only about 25-33 per cent as long as base of second dorsal; eye more than 50 per cent as long as snout in front of mouth ..... *Euprotomicrus* Gill 1864. p. 126

Genus DALATIAS Rafinesque 1810

Dalatias Rafinesque 1810,[a] p. 10; type species *D. sparophagus* Rafinesque, Mediterranean, equals **Squalus licha* Bonnaterre 1788, designated by Jordan, Tanaka and Snyder 1913. For generic synonyms and references, see Bigelow and Schroeder 1948, p. 501.

Generic characters. Dalatiinae with blade-like lower teeth, the cusp erect, triangular, with serrate edges, the base quadrate with a conspicuous notch on the outer edge marking the transition from cusp to base. Snout in front of mouth much shorter than from mouth to level of first gill openings; longest gill openings about 8-11 per cent as long as head to origin of pectorals (specimens measured); lips only moderately expanded at corners of mouth, and without special cartilages, but conspicuously thick and fleshy inward along each jaw and close-set with a complex series of cross folds with finely fringed edges (Fig. 15, I); furrow from corner of mouth reaching rearward about 30 per cent of distance towards first gill openings; no preoral clefts, but with voluminous subdermal pouches extending forward from the oral pockets (Fig. 1E); caudal fin of the shape shown in Fig. 14A, its axis rather steeply raised; origin of first dorsal fin much nearer to rear edge of pectorals when these are laid back than to origin of pelvics; second dorsal fin about 1.3 times as long as first dorsal at base; no spine in either of the dorsal fins. Denticles on sides of body thick, quadrate, outer surface with three weak ridges united rearward in a point that varies

in length and in acuteness from denticle to denticle; denticles on lower side of snout overlapping, ovate, without marginal teeth (Bigelow and Schroeder 1948, Fig. 96, D, E).

Greatest recorded length, 1820 mm. (Duméril 1865, p. 452).

Depth range. Definite depths of capture that we have found recorded for *Dalatias* in one part of the oceans or another have ranged from about 90 meters down to 600 meters. Probably it is more numerous in the shoaler part of its vertical range, else fishermen would hardly be as familiar with it as they have long been in the eastern side of the North Atlantic, from northwestern Africa and the Canaries to the Irish slope; also in the Mediterranean.

Remarks. The serrate lower teeth of *Dalatias,* and the shape of its caudal fin, with its conspicuously fleshy and complexly sculptured lips, set it so sharply apart that there is no danger of confusing it with any other genus of Dalatiinae.

Species. It is probable that all the reports for *Dalatias* that have appeared in scientific literature during the past century and a half have been based on the single species **D. licha* (Bonnaterre) 1788, type of the genus, which was originally described from "Cap Breton" on the coast of Brittany, by Broussonet (1780, p. 677), as "La Liche." In the eastern side of the Atlantic, **licha* is now known to be generally distributed from tropical West Africa (Rio de Oro), Morocco, the western Mediterranean, the Canaries, and Madeira to the Irish Atlantic slope and to the fishing grounds west of Ireland. Contrasting with this widespread occurrence, and with its local abundance in the Mediterranean and near Ireland, there have been only two published records of its capture in the western Atlantic, the one for a female of about 5 feet (about 1550 mm.), taken on Georges Bank, August 19, 1937 (Nichols and Firth 1939, p. 85; Bigelow and Schroeder 1948, p. 502); the other for an 845 mm. female from the northern part of the Gulf of Mexico (Bigelow, Schroeder and Springer 1955, p. 10). But the recent capture by "Oregon" of a female only about 380 mm. long (U. S. Nat. Mus. No. 157844) in the northern side of the Gulf, suggests that the latter may harbor a resident population.

**D. licha* has also been reported under its own name by Smith (1949, p. 56) from southern Africa, whence it had previously been recorded as a separate species (*D. brevipinnis* Smith

1936, p. 1); from New Zealand; from Australia; also from Japan both as *licha* and as *americanus* Gmelin 1789 (an obvious synonym for *licha*). Identification as *licha* in the case of the Japanese form is corroborated by our own comparison of a Japanese specimen with the specimens we have seen from Georges Bank and from the Gulf of Mexico. (For the list of New Zealand, Australian and Japanese references for **licha,* see Bigelow and Schroeder 1948, p. 508.) Nor do we find anything in Herre's (1935, p. 124) account of the Japanese shark for which he proposed the new generic and specific names *Pseudoscymnus bohuensis* to suggest that it differs in any way from **D. licha.* And this applies equally to McCulloch's (1914, p. 81, Pl. 14) excellent account and illustration of the Australian shark that he described as "*licha*" but which Whitley (1931, p. 310; 1940, p. 151) rechristened *phillippsi,* although without including any supporting evidence to justify the new specific name.

With the known range of **D. licha* so extensive, it seems astonishing that the genus has not been reported as yet from the eastern side of the Pacific, south or north, or from the southern Atlantic, though it is known from Algoa Bay, southeastern Africa.

Genus SOMNIOSUS Lesueur 1818

Somniosus Lesueur 1818, p. 222; type species *S. brevipinna* Lesueur, Massachusetts, equals **Squalus microcephalus* Bloch and Schneider 1801.

For generic synonyms, see the list given by Bigelow and Schroeder 1948, p. 514, with the addition of *Heteroscymnus* Tanaka 1912, type species *H. longus* Tanaka, Japan (see p. 121).

Generic characters. Dalatiinae, without fin spines; teeth smooth edged, the lowers with the cusp directed so strongly outward in some species that the inner edges function as a nearly unbroken cutting edge parallel with the jaw, but more nearly erect in others (Pl. 3); snout in front of mouth at least not longer than from mouth to level of first gill openings; longest gill openings about 9-11 per cent as long as head to origin of pectorals on specimens measured; lips not conspicuously thick, their surface smooth; furrows from corners of mouth reaching rearward only about 35-40 per cent of the distance toward first gill openings; no preoral clefts but with voluminous preoral pouches extend-

ing forward from oral pockets; caudal fin with upper division widely expanded, as well as the lower (Fig. 14B); upper margin about 1.5 times as long as lower anterior margin. Caudal axis moderately raised. Origin of first dorsal fin nearer to rear edge of pectorals (when these are laid back) than to origin of pelvics; second dorsal fin not larger than the first dorsal; interspace between first and second dorsal fins 1.7-3 times as long as between second dorsal and caudal; denticles on sides of body conical to thorn-like, curved rearward, differing widely in size from species to species, and in degree of elevation from the skin.

Size. The different species of *Somniosus* differ widely in size. Thus *rostratus* is not known to grow longer than about one meter. But *microcephalus* averages 8-14 feet (2.4-4.3 meters) at maturity, with specimens of 16-18 feet (4.9-5.5 meters) taken occasionally, and one of 21 feet (6.4 meters) definitely recorded (see Bigelow and Schroeder 1948, p. 519 for further information).

Depth range. The best known member of the genus (**microcephalus*, p. 117) has long been known to occupy a wide depth range, coming right up to the ice in the northern part of its range (Greenland, Labrador) in winter, but in summer most often caught at 180-550 meters, with one recorded from 1207 meters. (For further details see Bigelow and Schroeder 1948, p. 521.) And the depth range is, presumably, about the same for its representative in the North Pacific (*pacificus*, p. 121), though precise information is lacking. The only definite depth record we find for *S. rostratus* of the eastern Atlantic, said by Tortonese (1937-1938, p. 75) to occur off Portugal in shoal water as well as deep, is about 1000 meters, near Madeira, by line fishermen's report (Maul, 1955, p. 7). And the only information at hand in this respect for **S. longus* of Japan (p. 121) is that the specimens so far seen were the product of the deep hook and line fishery in Sagami Bay, Tanaka 1912a, p. 104).

Remarks. The combination of a very short snout with a caudal of the shape shown in Figure 14B, a first dorsal fin originating near the mid-length of the trunk, a second dorsal not larger than the first, and thorn-like denticles, with lower teeth more or less strongly oblique, and razor sharp, makes the recognition of

a *Somniosus* easy, even as one is dumped on deck from the trawl.

The caudal fin in *Somniosus* has a distinct subterminal notch in the specimens we have seen from the Gulf of Maine, from Iceland, and from Japan; indeed it has been so pictured for *rostratus* by Burkhardt (1900, p. 564, Fig. 3) and by Helbing (1904, Pl. 9, fig. 1); for **microcephalus* by Helbing (1904, Pl. 9, fig. 2, as "*borealis*"); by Garman (1913, Pl. 15, fig. 4), and by Bigelow and Schroeder (1948, Fig. 100); by Tanaka (1912a, Pl. 26) for **longus*. Since it is similarly notched on the type specimen of **S. pacificus* Bigelow and Schroeder 1944, from Japan (pictured by Garman 1913, Pl. 15, fig. 1, under the name "*brevipinna*"), we suspect that Tanaka's (1911, Pl. 11, fig. 32) earlier illustration of it for that species (under the name *microcephalus* Bloch and Schneider 1801) as without a notch, represents the result either of wear, or of mutilation.

More significant from the taxonomic standpoint is the wide expansion of the fin above the caudal axis, and its sublunate shape (Fig. 14B).

One species (*rostratus* of the Mediterranean and adjacent Atlantic) is brilliantly luminescent. For a first hand account of its luminescence, and of its light-producing organs, see Burkhardt 1900, p. 560.

Species. The following named species (listed here in chronological order) fall in *Somniosus*:

**Squalus microcephalus* Bloch and Schneider 1801, boreal-subarctic latitudes in the eastern Atlantic; **Somniosus brevipinna* Lesueur 1818, corresponding zone in the western North Atlantic; *Scymnus rostratus* Risso 1826, Mediterranean and Madeira; **Heteroscymnus longus* Tanaka 1912, Japan; *Somniosus antarcticus* Whitley 1939, Macquarie Island, Subantarctica, south of Australia; **Somniosus pacificus* Bigelow and Schroeder 1944, Japan, probably also northeastern Asiatic coast, and American coast from Bering Strait southward to Puget Sound, occasionally to southern California.

Our own comparison of a 1334 mm. male, taken off the coast of Massachusetts, with a 1564 mm. male from Iceland corroborates the view, now generally held, that the Greenland sharks of the subarctic on the two sides of the Atlantic (including the White Sea) and of the neighboring parts of the Arctic Ocean

belong to a single species. How closely the population of **S. microcephalus* in the two sides of the North Atlantic agree in proportional dimensions appears from the following tabulation: A, for a male, 1334 mm. long taken near Boston Lightship in 32 fathoms (Mus. Comp. Zool. No. 39609) and B, for a second male, 1564 mm. long, taken northwest of Iceland, Lat. 66°48′N., Long. 25°10′W., in 180 fathoms, October 1952 (Mus. Comp. Zool. No. 37826).

Proportional dimensions in per cent of total length

	A	B
Snout length in front of: outer nostrils	3.1	2.4
eye	7.3	6.4
mouth	10.3	9.3
Eye: horizontal diameter	2.2	2.4
Mouth: breadth	6.7	7.2
Nostrils: distance between inner ends	3.9	3.4
Gill opening lengths: first	1.8	2.0
second	2.0	2.2
third	2.0	2.2
fourth	2.0	2.2
fifth	1.8	2.0
First dorsal fin: vertical height	3.4	3.5
length of base	7.6	8.4
Second dorsal fin: vertical height	2.9	2.6
length of base	6.6	5.8
Caudal fin: upper margin	20.5	20.6
lower anterior margin	14.9	15.0
Pectoral fin: outer margin	12.1	13.2
inner margin	6.0	5.6
greatest width	6.5	6.2
Distance from snout to: first dorsal	41.2	38.0
second dorsal	65.3	64.9
upper caudal	79.5	79.4
pectorals	24.6	24.6
pelvics	59.7	59.3
Interspace between: first and second dorsals	16.5	18.3
second dorsal and upper caudal	7.7	8.7
pelvics and lower caudal	12.1	11.6
Distance between origins of: pectorals and pelvics	35.2	34.8
pelvics and subcaudal	17.1	17.0
Teeth:	48/48	45/51

This joint species was originally described by Gunnerus in 1766 under the name *Squalus carcharias,* but by the rules of nomenclature, it must be called **microcephalus* Bloch and Schneider 1801, "the name *Squalus carcharias* having been used previously by Linnaeus 1758, for a very different shark" (Bigelow and Schroeder 1948, p. 515). The known range of **microcephalus* extends from the White Sea, Bear Island, Spitzbergen and east and west Greenland, southward to the North Sea (to the mouth of the Seine as a straggler) in the east, to the Gulf of Maine in the west.

A second North Atlantic species, *rostratus* Risso 1826, resembles **microcephalus* so closely in general appearance that as recently as 1928 Rey (1928, p. 480), following Garman (1913, p. 241), classed it as identical with the former, while — to further confuse the issue — recent illustrations of *rostratus* by Burkhardt (1900, p. 564, fig. 3) and by Maul (1955, Pl. 3, fig. 17) differ as to the length of the upper side of the caudal peduncle relative to the length of the base of the second dorsal fin. Both, however, like Canestrini (1864, Pl. 2, fig. 2) and Helbing (1904, Pl. 9, fig. A) show the distance from the rear tip of the second dorsal to the origin of the upper side of the caudal as less than 70 per cent as long as the base of the second dorsal (about as long as the base of the second dorsal in **microcephalus*). A more important difference is that the lower teeth are pictured as with the cusp more nearly erect in *rostratus* (Fig. 15D, see also Maul 1955, Pl. 3, fig. 19) than they are in **microcephalus* (Pl. 3), and its denticles as rising less steeply from the skin (cf. Maul 1955, Pl. 3, fig. 20, with Bigelow and Schroeder 1948, fig. 101B).

Rostratus is also much the smaller member of the pair, the greatest length we find definitely recorded for it being only 1000 mm. (Helbing 1904, p. 347); whereas adults of **microcephalus* average 8-14 feet (2.4-4.3 meters) long, with a few growing considerably larger still (p. 116). A further difference already remarked upon by Burkhardt (1900, pp. 561-562, 565) is that while the luminescent organs of *rostratus* (p. 117) are surrounded and thus rendered conspicuous by denticles that differ in blunter cusps and more definitely stellate bases from those elsewhere on the sides, this is not the case in **microcephalus,* as we can verify from our own examination of a well

preserved male 1334 mm. long, taken off Massachusetts. For that matter, we have not been able to detect anything suggestive of luminescent organs on it, or on a 1564 mm. male from Iceland (p. 118).

Helbing (1904), also, in his extensive treatise on the anatomy and systematic relationships of *Somniosus* (as "*Laemargus*"), has pointed out several skeletal differences between *rostratus* and **microcephalus* (as "*borealis*"). Finally, *rostratus* is ovoviviparous (see Helbing 1904, p. 358, for illustration of its embryos at successive stages in growth), as are all the other genera of Squaloidea for which the mode of development is known, whereas it is still an open question whether **microcephalus* is ovoviviparous or oviparous (for a summary of available evidence, see Bigelow and Schroeder 1948, p. 520).

For a more detailed discussion of the differences in proportional dimensions between *rostratus* and **microcephalus*, see Tortonese 1937-1938, p. 74.

It has recently been suggested by Maul (1955, p. 9) that the Portuguese shark described and pictured under the name *rostratus* by Capello (1870, p. 148, Pl. 9, fig. 2) actually represents a third Atlantic species of *Somniosus* (as yet unnamed), for it is shown and described as differing from *rostratus* in a longer snout and head, and as with the position of the second dorsal fin different in relation to the pelvics, to which we may add a longer caudal pedunele. This appears from the following comparative dimensions of (A) *rostratus* according to Maul (1955, measurements, p. 9, and fig. 17), and of (B) the Portuguese specimen reported under that name, from Capello's measurements, and illustration, also measurements, contributed by Dr. A. M. Ramalho, who kindly re-examined the specimen now in the Bocage Museum in Lisbon.

	A	B
Length of head, to pectorals, in per cent of total length	20	28-29
Snout to mouth, in per cent of length of head	25	35
Distance from rear end of base of 2nd dorsal to upper origin of caudal, in per cent of total length	7	11

Also, the origin of the second dorsal, pictured as opposite the rear end of the bases of the pelvics by Maul, for his Madeira specimen, is about 10 mm. posterior to the pelvics on the Capello specimen, as we are informed by Dr. Ramalho, while excellent photographs of its mouth, supplied by him (Fig. 15E) show its lower teeth as somewhat more strongly oblique than they are pictured for the typical *rostratus* (Fig. 15D after Canestrini, 1864, Pl. 2, fig. 4; see also Maul 1955, fig. 19), i.e., resembling, rather, those of *microcephalus*. Thus, present indications are that the Capello specimen may well represent an undescribed species more nearly related to **microcephalus* than to *rostratus*. But it seems to us wiser to leave the matter open than to burden shark literature with a new name that might soon be relegated to oblivion.

The early reports of *Somniosus* from the North Pacific, west and east, were either as "*microcephalus*" or as "*brevipinna,*" on the assumption that the Pacific representative of the genus was identical with the Atlantic **microcephalus*. And the Japanese specimen, on which we based our new species *pacificus* (described and pictured by Garman 1913, p. 240, Pl. 15, figs. 1-3, as "*brevipinna*"), agrees with **microcephalus* (p. 117) in lacking any evident dermal structures to which a luminescent nature might be ascribed, and in the shape of its lower teeth. But its first dorsal stands considerably farther rearward than on the Atlantic specimens that we have seen of **microcephalus*, or than is pictured for *rostratus;* the distance from the tip of its second dorsal to the origin of the upper side of its caudal is shorter relative to the size of the second dorsal; the upper posterior and lower anterior margins of its caudal are more convex; and its upper teeth are broader. It was because of these differences that we proposed the new species **pacificus* for it (Bigelow and Schroeder 1944, p. 35). And it seems reasonably certain (though not yet proven) that the various reports of *Somniosus* from northeastern Asia, Alaska, and thence southward along the Pacific Coast of America to California all were based on this same species.

Japanese waters also harbor a second *Somniosus* (Fig. 15A, B, C, Pl. 3), the **Heteroscymnus longus* of Tanaka 1912a (p. 102, Pl. 26, figs. 102-107), more nearly resembling *rostratus* than either **microcephalus* or **pacificus* in the shape of its lower

teeth, in the minuteness of its denticles, and in the length of the base of its first dorsal fin relative to the length of the head. So closely, indeed, does Tanaka's account of its type specimen, corroborated by our examination of a female of about 1010 mm. (in rather poor condition), received from Dr. Tokiharu Abe, agree with the published accounts of *rostratus* (we have not seen that species) that it is doubtful whether the Japanese population differs consistently enough in any respect from the Atlantic population to deserve a separate specific name — final decision is a matter for the future.

Somniosus has not been reported from tropical-equatorial waters. But the *microcephalus-pacificus* division of the genus is represented in subantarctic latitudes by *S. antarcticus* Whitley 1939, a name proposed for an "8 foot, 2 inch" (2491 mm.) specimen that was found stranded on the beach at Macquarie Island in latitude about 54°49′S., south of Australia (Waite 1916, p. 51, fig. 10).

The position of its first dorsal fin, as pictured by Waite, and the shape of its caudal suggests a closer resemblance to **microcephalus* of the northern Atlantic than to **pacificus*. But final decision as to its specific relationship must await a more detailed study of the Southern Hemisphere population.

Key to Species of *Somniosus* in the Northern Hemisphere

1. Lower teeth only moderately oblique (Fig. 15D); adults with evident luminescent organs, at least in best known species (see p. 117) ..... *rostratus* Risso 1826. Mediterranean and Madeira; p. 119; also *longus* Tanaka 1912a, Japan, perhaps not distinguishable from *rostratus*, see discussion, p. 121.

   Lower teeth so strongly oblique that the inner margins are almost parallel with the trend of the jaw, forming a nearly uninterrupted cutting edge (Pl. 3); no evident luminescent organs 2

2. Head to pectorals 28-30 per cent of total length; lower teeth as in Fig. 15E .....*rostratus* Capello 1870 (*not* of Risso 1826), off Portugal; see discussion, p. 120.

   Head to pectorals only about 24-26 per cent of total length 3

3. Origin of first dorsal much nearer to tip of snout than to tip of caudal; interspace between first and second dorsals as long as from snout to 1st-2nd gill openings or longer .....

**microcephalus* Bloch and Schneider 1801. Both sides of northern North Atlantic. p. 117.

Origin of first dorsal almost as near to tip of caudal as to tip of snout; interspace between first and second dorsals only about 66 per cent as long as from tip of snout to second gill openings .....

**pacificus* Bigelow and Schroeder 1944. Type locality Japan, probably also northeastern Asia and Pacific Coast of North America, from Bering Sea south to Puget Sound, occasionally to southern California. p. 121.

Genus ISISTIUS Gill 1864

Isistius Gill 1864, p. 264; type species **Scymnus brasiliensis* Quoy and Gaimard 1824, off Brazil.

Generic characters. Dalatiinae without dorsal fin spines; lower teeth symmetrically triangular and smooth-edged, or only faintly and irregularly serrate; snout in front of mouth shorter than from mouth to first gill openings; lip fold at corners of mouth smooth but greatly expanded (Fig. 1F; Bigelow and Schroeder 1948, fig. 98B), and supported by special cartilages that are easily felt; groove at corners of mouth extending rearward for about half (44-57 per cent) of the distance toward first gill openings (Bigelow and Schroeder 1948, fig. 98B); no preoral clefts, but with voluminous subdermal pouches extending forward from oral pockets (Fig. 1F); gill openings minute, only about 4.3-4.4 per cent as long as head to origin of pectorals on western North Atlantic and Japanese specimens measured; rear end of base of first dorsal fin about abreast of origin of pelvics; second dorsal only very slightly longer at base than first dorsal (1.2 times on specimens measured); interspace between first and second dorsal fins only about 50 per cent as long as between pelvics and lower origin of caudal; caudal fin sublunate, with well-marked subterminal notch, nearly or quite as broad above caudal axis as below, its upper margin about 1.5 times as long as lower anterior margin; the caudal axis raised only very

slightly. Denticles on sides of body truncate, with concave crown.

Maximum recorded length close to 500 mm. (Bigelow and Schroeder 1948, p. 512).

Range. Tropical and subtropical belts of Atlantic, Pacific and Indian Oceans.

Remarks. It has long been common knowledge that the sole known representative of *Isistius* (**brasiliensis* Quoy and Gaimard 1824) is brilliantly luminescent, the entire lower surface of its body (except for the dark collar) shining with a vivid greenish light that presumably is produced by black dots with which the lower surface is strewn densely; the sides, the dorsal and caudal fins, and the basal parts of the pectorals more sparsely so (see Bennett 1840, p. 225, for an eye-witness account of the luminescence; Burkhardt 1900, pp. 555, 556, 565, fig. 5 for the distribution of luminescent dots).

Species. The various reports that have come to hand for *Isistius* from one part of the ocean or another seem all to have been based on the one species that was described first by Quoy and Gaimard (1824, p. 198) from Brazilian waters as **Scymnus brasiliensis*. *Brasiliensis* has subsequently been taken in the Gulf of Guinea, off Sierra Leone and Cape Verde, and north of the Bahamas in the Atlantic; near the Galapagos and the Hawaiian Islands, in Japanese waters, near Fiji, west of Christmas Island, north of New Guinea, near Lord Howe Island off New South Wales, between Java and western Australia and near Mauritius in the Pacific and Indian Oceans. Recent records for the mid-Pacific are of three specimens, taken at the surface in the equatorial belt southward from the Hawaiian group (Lat. 2°04′S, Long. 168°57′W; Lat. 4°47′N, Long. 161°04′W; and Lat. 2°09′N, Long. 158°14′W) where the water is 1000-3000 fathoms (about 1830-5485 meters) deep (King and Ikehara 1956, pp. 18-19). (For a description and list of references, see Bigelow and Schroeder 1948, pp. 509-514, figs. 98-99.)

Genus SCYMNODALATIAS Garrick 1956

Scymnodalatias Garrick 1956, p. 564; type and only known species, *Scymnodon sherwoodi* Archey 1921, p. 195, Pl. 39, New Zealand.

Generic characters. Dalatiinae without dorsal fin spines but

with distinct preoral clefts (see discussion, p. 12); teeth smooth-edged, the uppers "needle-like, with asymmetrically twisted cusps" (Garrick 1956, p. 564), the lowers with triangular cusp much more nearly erect than in *Somniosus;* snout in front of mouth only about as long as from mouth to first gill openings; head to pectorals between 20 and 25 per cent of total length; longest gill openings pictured as about 9 per cent as long as head to pectorals; lips at corners of mouth not conspicuously expanded; furrow from corners of mouth reaching rearward only about 17-20 per cent of distance toward first gill openings; pre-oral clefts, described by Garrick (1956, p. 568) as "upper labial furrows," short, but clearly shown on Garrick's (1956, Pl. 1, figs. A, C) illustrations of type specimen; whether or not expanded inwardly is not known. Caudal fin with distinct subterminal notch; upper margin about twice as long as lower-anterior margin; caudal axis moderately raised; origin of first dorsal fin far in advance of pelvics; second dorsal fin a little larger than first dorsal; interspace between first and second dorsal fins about twice as long as between second dorsal and caudal; denticles on sides below first dorsal fin scale-like, overlapping, the free margins strongly tridentate, with median point considerably the longest, the outer surface with three ridges corresponding to the marginal points.

Size. The state of development of the claspers of a male *sherwoodi,* 803 mm. long (only specimen yet seen) makes it likely that this shark matures sexually when it is 900-1000 mm. long.

Range. So far known only from New Zealand.

Remarks. Archey's (1921, p. 195) original account of *sherwoodi* credits it with dorsal fin spines in the form of "scarcely discernible rudiments imbedded in the skin." Garrick (1956, p. 556), however, on examining the type specimen was unable to find any indication whatever of a spine in either dorsal fin, even on dissection, nor any indication that spines might have been removed. Seemingly what Archey interpreted as spines actually were the "most anterior of the radial cartilages supporting the dorsal fins" (Garrick 1956, p. 556). It is for this reason that we follow Garrick in placing *Scymnodalatias* among the Dalatiinae, rather than among the Squalinae, where Archey (1921) originally located it. Actually it bridges the gap

between the two subfamilies, having a well marked preoral cleft reaching forward from each corner of the mouth (for discussion, see p. 12), and in having upper teeth longer in the middle third of each side of the jaw than either toward the center of the jaw or toward its outer corner, as is true of *Scymnodon* (p. 96).

Scymnodalatias resembles the Japanese **Somniosus longus* (Tanaka 1912a, p. 102) in its bodily proportions in general, as well as in the sizes, shapes and relative positions of the dorsal, pelvic and pectoral fins, and in the shape of its lower teeth. But it differs sharply from all members of the genus *Somniosus* in the shape of its caudal fin (see key, p. 112), and especially in having well marked preoral clefts (see above under Generic Characters). Other differences, seemingly generic, to which Dr. Garrick has called our attention in a recent letter are that the second dorsal fin is larger than the first in *Scymnodalatias*, that the first dorsal stands farther rearward, and that its lower teeth are more erect.

Species. Only one species referable to *Scymnodalatias* has yet been reported, namely the *Scymnodon sherwoodi* of Archey 1921, so far known from a single specimen found on the beach near Canterbury, New Zealand, in 1920. For a detailed and well illustrated account of it, with discussion of its systematic relationships, see Garrick 1956.

Genus EUPROTOMICRUS Gill 1864

Euprotomicrus Gill 1864, p. 264, footnote 4, type species *Scymnus* (*Laemargus*) *labordii* Müller and Henle 1841, p. 94, Islands of Mauritius and Bourbon, Indian Ocean; equals **Scymnus bispinatus* Quoy and Gaimard 1824, p. 197, Pl. 44, figs. 1, 2.[27]

Generic characters. Dalatiinae without dorsal fin spines; the snout blunt, its length in front of mouth about as great as from mouth to level of third gill openings; caudal pedunele without precaudal pits. Head to pectorals between 20 and 25 per cent of total length; lips at corners of mouth thick, fleshy, whether or not with supporting cartilages is not known; no preoral clefts, but with a voluminous pouch extending forward from

[27] In replacing Quoy and Gaimard's (1824) name **bispinatus* with *labordii*, Müller and Henle formalized Quoy and Gaimard's use of "Leiche laborde" as the French vernacular name for this shark, proposed in memory of M. Theodore Laborde.

each oral pocket; groove from corner of mouth reaching rearward for 50-66 per cent of the distance toward first gill openings; gill openings minute (Fig. 16F). First dorsal fin considerably posterior to mid-length of trunk, but its base well in advance of origin of pelvics; second dorsal about 2.5 times as long, at base, as first dorsal; interspace between first and second dorsals a little longer than between second dorsal and caudal; caudal fin without subterminal notch, its upper margin about 1.2 times as long as lower-anterior margin; caudal axis moderately raised and continuing to extreme rear margin of the fin; the fin wider below the axis than above; dermal denticles described as low, quadrate, with concave crowns and of two sizes (Hubbs and McHugh 1951, p. 167), the smaller much the more numerous, the larger with stellate bases, and with additional pits surrounding the axial concavity.[28] Teeth smooth edged; the uppers slender, symmetrical, slightly recurved; the lowers with cusp directed obliquely outward, the successive inner edges at an angle of about 45° with the jaw.

Luminescence. The single known species of *Euprotomicrus* is one of the few sharks that are known to be luminescent, glowing, as described by Dickens (1956), with a greenish light that is given off from its lower surface by "many thousands of small light organs," according to Marshall (1956, p. 73).

Size. Lengths of 233 mm. reported by Hubbs and McHugh (1951, p. 170) and of "8-9 inches" by Günther (1870, p. 428) for the only known species of the genus probably approximate the maximum to which it ordinarily grows, for Duméril (1865, p. 457) described the claspers of a male of 205-210 mm. as having a strong spine on the outerside, i.e., as close to maturity. Similarly, the gravid female, 234 mm. long,[29] recently reported by Dickens (1956) and by Marshall (1956) gave premature birth to six young when brought on board ship. Thus *Euprotomicrus* falls in the same size-group with *Squaliolus* (p. 129) and with the smaller of the species of *Etmopterus* (p. 48).

Species. All the various reports for *Euprotomicrus* (see Garman 1913, p. 235 for synonyms under *bispinatus* Quoy and Gai-

[28] We have detected the smaller denticles alone on the specimen we have seen, and only a few of these, here and there. Seemingly its skin has been largely denuded of its armature.

[29] Information contributed by Mr. N. B. Marshall.

mard 1824 and *E. hyalinus* Eigenmann 1891) seem certainly to have referred to the type species *bispinatus* Quoy and Gaimard 1824, of which we have been fortunate enough to study a female, 161 mm. long, from the North Pacific, west of Johnston Island. For a description of it, with measurements, see King and Ikehara 1956, p. 17. For a description of a somewhat larger female (233 mm. long) taken in 1948 some 500 miles off California, with excellent illustrations, and with discussion of the relationships of the genus, see Hubbs and McHugh 1951. The most recent report is that of a gravid female 234 mm. long, taken from the SS "Kent" in the southern Indian Ocean west of Australia, Lat. 23°10′S., Long. 101°58′E. (Dickens 1956; Marshall 1956).

E. bispinatus is known from the Indian Ocean, near Mauritius and Bourbon as well as west of Australia (see above), from New Zealand waters, from the northern Pacific localities mentioned above, and from between Honolulu and San Francisco (Eigenmann 1891, p. 35, as *E. hyalinus*). Our earlier reference of the genus to the Philippines (Bigelow and Schroeder 1948, p. 500) was based on the misconception that the generic name *Squaliolus* Smith and Radcliffe 1912 is an equivalent.

Evidently this is a pelagic species; the specimen we have seen (see above), the one described by Hubbs and McHugh and the one reported by Capt. Dickens (1956) having all been picked up at the surface at night, where the water is more than 2000 fathoms (about 3660 meters) deep.

Genus SQUALIOLUS Smith and Radcliffe 1912

Squaliolus Smith and Radcliffe, 1912, p. 683. Type species **S. laticaudus* Smith and Radcliffe 1912, p. 685, Pl. 50, Philippines.

Generic characters. Dalatiinae with a short spine in the first dorsal fin, either exposed at the tip (Fig. 16A, D) or wholly enclosed in the skin, but without a spine in the second dorsal fin; snout in front of mouth nearly or quite as long as from mouth to origin of pectorals; head, to pectorals, about 33 per cent of total length; caudal peduncle without precaudal pits; lips at corners of mouth thick and fleshy, as in *Euprotomicrus* (p. 126); no preoral clefts, but with a voluminous pouch extending forward from each oral pocket (Fig. 16C); furrows from corners

of mouth reaching rearward 50-70 per cent of the distance toward first gill openings (Fig. 16A, B). Base of first dorsal spine considerably posterior to a perpendicular at axil of pectorals; second dorsal fin at least twice as long at base as first dorsal, its rear tip reaching to a point about midway between rear end of base of second dorsal and origin of upper side of caudal. Caudal fin sublunate, with bluntly pointed tips and without subterminal notch; upper margin only slightly longer than lower anterior margin; the maximum width of the fin nearly as great above the axis as below (Fig. 16A); caudal axis not raised, except that the extreme tip curves upward at the margin of the fin (Fig. 16A). Teeth smooth edged, uppers slender, symmetrical, somewhat recurved, lowers with cusps directed obliquely outward, the inner edges weakly concave in outline, making an angle of about 33° with the jaw (Fig. 16C); the general contour of the tooth deeply notched on the outer side marking the transition from cusp to base. Dermal denticles rather closely spaced and so prominent that the skin has a pebbled look (Pl. 4), truncate, with concave crowns (Fig. 15H), on four-radiate bases, and varying in size from denticle to denticle.

Size. The type species, *laticaudus*, matures when only about 150 mm. long, to judge from the stage in development of the claspers of the type specimen (Smith and Radcliffe 1912). Thus *Squaliolus* includes the smallest shark for which the size at maturity is known, though it is closely rivalled by *Euprotomicrus* (p. 127), by the smaller of the species of *Etmopterus* (p. 48); also by the smallest of the members of the family Scyliorhinidae among the galeoid sharks. *Sarmenti,* the second known species of *Squaliolus*, grows somewhat larger, the two specimens yet seen having measured 224 mm. and 226 mm. in length (both were females).

Depth range. The two specimens of the type species (*laticaudus*) that have yet been seen were taken in Philippine waters in a beam trawl dragging at about 310 meters (170 fathoms, Smith and Radcliffe 1912, p. 685); they may, of course, have been picked up by the trawl either on its way down or on its way up again (p. 5). The case of the second known species is puzzling, for while the original specimen was caught near Madeira on a long line, presumably fishing at least as deep as

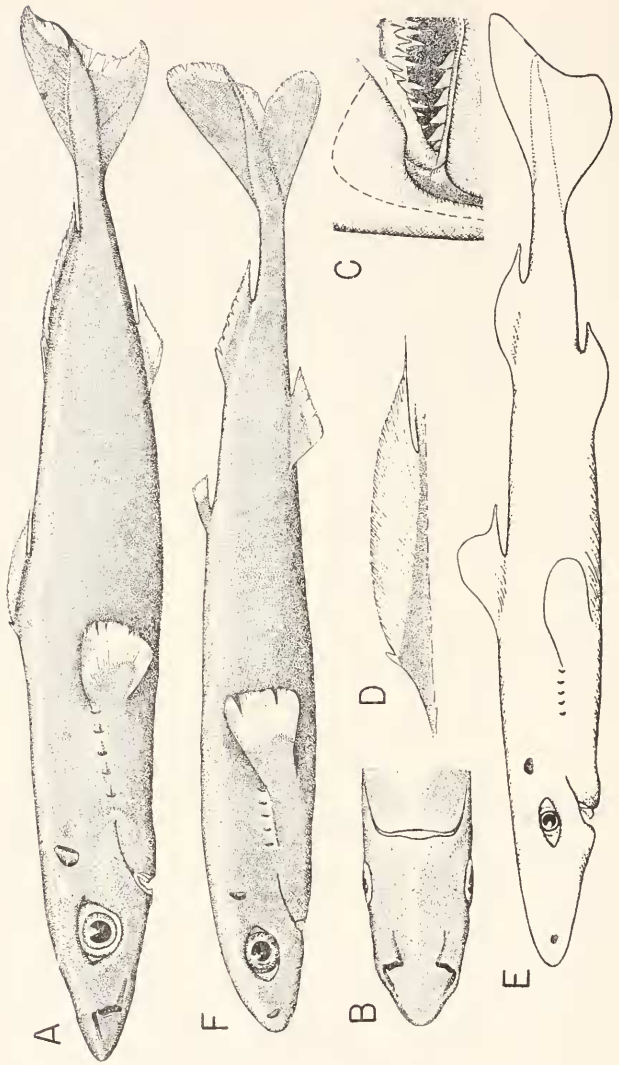

FIGURE 16

900 meters or so (Noronha 1926), the second known specimen was caught in very shoal water, near Arcachon, France, among eel grass (Zostera). (For details see Sigalas 1939-40, p. 70.)

Remarks. In our earlier synopsis of the dalatiine sharks (Bigelow and Schroeder 1948, p. 500, footnote 2) we classed *Squaliolus* as a synonym of *Euprotomicrus,* as had Garman (1913, p. 234) and Fowler (1941, p. 264). Recent examination, however, of the type specimen of *laticaudus* (in the U. S. National Museum), and of the female pictured on Figure 16A has convinced us that *Squaliolus* is separable generically from *Euprotomicrus* from which it is set apart not only by the presence of a spine in the first dorsal fin (it differs in this from all other Dalatiinae for that matter), but also by the position, much farther forward, of its first dorsal fin, by its much longer and more pointed snout, and by its conspicuously longer head.

In the type species each nostril is prolonged at the outer end by a conspicuous groove directed forward, and at the inner end by a similar groove directed rearward (Fig. 16B). But we hesitate to include this feature among the generic characters, because the condition in this respect is not known for the second known representative of the genus (*S. sarmenti,* see below).

Species. Two species referable to *Squaliolus* are known, **S. laticaudus* Smith and Radcliffe 1912, (from the Philippines), type of the genus, and *S. sarmenti* Noronha 1926, which was originally described from Madeira, and which has recently been reported from Arcachon, France, by Belloc (1937) and by Sigalas (1939-40). The chief difference between these two is that while the tip of the first dorsal spine is exposed in **laticaudus* (Fig. 16A, D), it is described by Noronha as entirely enclosed in the skin in *sarmenti.* Other differences mentioned by Noronha

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Fig. 16. A, *Squaliolus laticaudus,* female, 143 mm. long, Philippines, U. S. Nat. Mus., No. 70259. B, ventral view of anterior part of head of same. C, right hand corner of mouth of same, the preoral pouch indicated by the broken curve, x about 4. D, first dorsal fin of same, to show spine, x about 3. E, *Heteroscymnoides marleyi,* after Fowler, slightly emended from comparison with the type specimen, a female, 126 mm. long, from the Durban Coast, southern Africa (see p. 133). F, *Euprotomicrus bispinatus,* female, 161 mm. long, from central Pacific west of Johnson I., U. S. Nat. Mus. No. 164176.

are that the first dorsal fin stands a little farther forward in *sarmenti*, in which the distance from snout to first dorsal origin is about 42 per cent as long as the trunk (about 48 per cent in **laticaudus*), and that the pectorals, when laid back, reach only about as far as the concealed first dorsal spine in *sarmenti*, but overlap the base of the fin in **laticaudus*. It may also prove that *S. sarmenti* lacks the grooves extending from the inner and outer ends of the nostrils that characterize **S. laticaudus*, for they are not indicated on the illustrations of *sarmenti* (Noronha 1926, Pl. 35). But the latter are not clear in this respect.

Genus HETEROSCYMNOIDES Fowler 1934

Heteroscymnoides Fowler 1934, p. 239, type species **H. marleyi* Fowler 1934, p. 240, Durban coast, southeastern Africa.

Generic characters. Dalatiinae without fin spines; snout in front of mouth about as long as from mouth to third gill openings; head (to pectorals) more than ⅓ of trunk (to origin of caudal); gill openings minute, not more than 3-4 per cent as long as head to origin of pectorals; lip at corners of mouth neither conspicuously thick and fleshy nor expanded; furrow at corners of mouth reaching rearward about 40 per cent of the distance toward first gill openings; no preoral clefts; whether or not with preoral pouches is not known; origin of first dorsal fin close behind a perpendicular at origin of pectorals; second dorsal fin about 1.2 times as long (at base) as first dorsal, its origin over bases of pelvics; distance from rear base of second dorsal to origin of upper side of caudal fin about 50 per cent as long as interspace between first and second dorsals; caudal (in excellent condition on the one known specimen) without subterminal notch, about 1.7 times as wide below caudal axis as above; upper margin about 1.3 times as long as lower anterior margin; caudal axis not appreciably raised. Dermal denticles on sides of body (Fig. 15G) triangular spur-like, with three prominent ridges, raised only slightly, on quadrate bases, and so closely spaced that the skin is almost wholly concealed. Upper teeth erect, lowers directed somewhat obliquely outward (Fowler 1941, p. 273).

The size at maturity is not known, the only specimen yet seen being a newly born female, 126 mm. long, with healed umbilical

scar. Presumably this was from shoal water, but the depth of capture is not known.

Remarks. The features that set *Heteroscymnoides* the most obviously apart from related genera are its long snout and head, minute gill openings, shape of caudal fin, and location of the first dorsal fin.

Species. One species only (the type) is known, **H. marleyi* Fowler 1934. For a detailed account, with illustration showing its general appearance, see Fowler's (1934, p. 239; 1941, p. 273) original description of the only specimen that has yet been seen. Having had an opportunity to examine the latter through the kindness of Dr. James Böhlke of the Academy of Natural Sciences, Philadelphia, we include the following table of its proportional dimensions as per cent of total length, with number of teeth.

Snout, length in front of: eye	11.9
mouth	17.1
Eye: horizontal diameter	4.8
Mouth: breadth	8.0
Nostrils: distance between inner ends	4.0
Gill openings: length of longest	1.0
First dorsal fin: vertical height	3.2
length of base	6.4
Second dorsal fin: vertical height	2.8
length of base	8.2
Caudal fin: upper margin	18.3
lower anterior margin	13.9
Pectoral fin: outer margin	10.7
Distance from snout to: first dorsal	34.1
second dorsal	65.8
upper caudal	81.7
pectorals	30.1
pelvics	57.5
Interspace between: first and second dorsals	22.2
second dorsal and caudal	10.0
Distance from origin to origin of: pectorals and pelvics	27.4
pelvics and caudal	21.4
Teeth:	6-1-6
	11-1-11

Subfamily ECHINORHININAE

Squalidae without fin spines; the teeth with several cusps, the median cusp much the largest; upper teeth similar to lowers; caudal axis raised, the fin wider below the axis than above, its tip pointed, without subterminal notch; short preoral clefts, but not expanded inwardly, nor is the pocket at each corner of the mouth extended rearward, furrow-like, as it is in all other known representatives of the family Squalidae; dermal dentieles either simple, with central cusp, or compound, with two or more cusps, and varying correspondingly in size on any given individual; lateral line, along sides of body roughened with series of minute thornlets (see *Remarks*, below). Recorded up to 8-9 feet long.

Echinorhinus Blainville 1816 is the only known genus.

Genus ECHINORHINUS Blainville 1816

Echinorhinus Blainville 1816, p. 121; type species *E. spinosus*, no author quoted but doubtless the **Squalus brucus* of Bonnaterre 1788, p. 11, intended.

For generic synonyms, see Bigelow and Schroeder 1948, p. 526.

Generic characters. Those of the subfamily.

Depth range. "In all warm seas from 10-100 fathoms" (18-183 meters), Smith 1949, p. 56.

Remarks. The combination of characters given above under the subfamily, especially the buckler-like dentieles, often with 2 or more cusps, and the peculiar armature of the lateral line, would place *Echinorhinus* at a glance, should one come to hand in any part of the world where it is not well known.

Accounts of the lateral line in *Echinorhinus* have been conflicting. Rey (1928, p. 488) who had seen only a dried skin, described it as in the form of a deep furrow enclosed between two close-set rows of slender tentacular structures or dermal papillae, though with the reservation that he could not form an exact idea of it. This is in line with McCoy's (1887, Pl. 144, fig. 1G, reproduced by Whitley 1940, fig. 169) illustration of it as flanked by two sparse rows of flexible papillae. And it was from these sources that our earlier account of it (Bigelow and Schroeder 1948, p. 527) was drawn. McCoy (1887, p. 165), however, described it for his Australian specimen as "roughened

with rows of minute, slender hooked spines" as far forward as the third gill openings. And it is similarly armed with minute, curved, thorn-like spines on an excellent specimen from the Mauritanian Coast that we have received through the kindness of Dr. Ramalho, the only suggestion of papillae or the like being that the course of the channel is marked by numerous shreds of skin and flesh, seemingly the result of wear. In its present state the canal is open along most of its length on both sides of the body. But as seen in cross-section its lower lip overlaps the upper. And since it is bridged over here and there for short stretches by the tissue-paper-thin skin, we assume that normally the canal is closed, at least as far rearward as the pelvic fins, if not farther still. A touch is enough to show that the spinelets are denticular structures, not fleshy. And they are in plain view (under a lens) wherever the canal is open. But we have not been able to determine (because of the condition of the specimen) whether they are exposed at the tips along the short stretches where the canal is roofed over, or whether they are entirely enclosed, as is suggested both by surface views and by cross sections of the canal.

Species. The following named species fall in *Echinorhinus:* **Squalus brucus* (Bonnaterre) 1788 (also reported repeatedly as *spinosus* Blainville 1825), the type of the genus, well known in the eastern North Atlantic; *Echinorhinus obesus* Smith 1849, Pl 1, South Africa; *E. cookei* Pietschmann 1928, p. 297; 1930, p. 3, Fig. 1, Hawaiian Islands; and *E.* (*Rubusqualus*) *mccoyi* Whitley 1931, p. 311, 1940, p. 151, Victoria, Australia. But Fowler (1941, p. 278) who examined a specimen of *cookei* in Honolulu could not find "that *Echinorhinus cookei* is other than a variant of **brucus*", nor can we find anything in the accounts of *obesus* or of *mccoyi* to suggest that they differ significantly from **brucus,* as represented by a specimen of the latter from the eastern Atlantic in the British Museum (Bigelow and Schroeder 1948, Fig. 102), and by a male 1600 mm. long, from the coast of Mauritania, recently received through the kindness of Dr. A. M. Ramalho. On this basis, the recorded range of **brucus* includes the eastern North Atlantic from tropical West Africa to Ireland and the North Sea (including the Mediterranean); the coast of Massachusetts in the western North At-

lantic (one specimen found washed ashore at Provincetown, Massachusetts, in 1878); South Africa; Argentina; California; the Hawaiian, Japanese, and Australo-New Zealand regions, and Arabian waters. (For further details and for references, see Bigelow and Schroeder 1948, pp. 529-532.)

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